

Historic, Archive Document

Do not assume content reflects current scientific knowledge, policies, or practices.



United States
Department
of Agriculture

Forest Service

Intermountain
Research Station

General Technical
Report INT-GTR-309

July 1994



Cot/Ind

Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge

AD5
UNIVERSITY



INTERNATIONAL WORKSHOP
ST. MORITZ 1992

48
Received by: JyB
Working Group
bw

Statements by contributors from outside the U.S. Department of Agriculture are solely the views of the authors and do not reflect policies or opinions of the Department.

The use of trade or firm names in this publication is for reader information and does not imply endorsement of any product or service by the U.S. Department of Agriculture or other organizations represented here.

Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge

St. Moritz, Switzerland, September 5-11, 1992

Compilers:

Wyman C. Schmidt
Intermountain Research Station
Forest Service
U.S. Department of Agriculture

Friedrich-Karl Holtmeier
Department of Geography
University of Münster
Germany

Workshop Sponsors:

Intermountain Research Station
Westfälische Wilhelms-Universität,
Landscape Ecology Division, Germany
Swiss Federal Institute for Forest, Snow,
and Landscape Research
Karl and Sophie Binding Foundation,
Switzerland



FOREWORD

This proceedings is a product of the first comprehensive and international examination of stone pine species of the world. It reports the papers that were presented at the International Workshop on "Subalpine Stone Pines and Their Environment—The Status of Our Knowledge" held September 5-12, 1992, at St. Moritz, Switzerland.

It is generally recognized that there are five subalpine stone pines in the world—all in the Northern Hemisphere—one in North America and four in Europe and Asia. All share many of the same characteristics and occupy similar ecological niches. Stone pines are defined as those species of *Pinus* that have five-needled fascicles, have wingless seeds, and have cones that remain closed at maturity.

How did this international workshop come about? Completion of a whitebark pine workshop in 1987 and a major symposium in 1989 in Bozeman, MT, U.S.A., sparked interest in high-elevation ecosystems of western North America. One section of this popular symposium specifically addressed high-elevation ecosystems of the world. Information presented there hinted that we could learn much about whitebark pine ecosystem analogs from other parts of the world that have similar physical and biological features. In addition many of the Eurasian forests have a long history of human influence. The logical place to look for this type of information was the world's forest areas that supported subalpine stone pines. A cursory examination of the five commonly recognized subalpine stone pines indicated they had many similarities.

With this as a background, a small group of western U.S. researchers and managers held a planning session with Dr. Holtmeier from Muenster, Germany, in Missoula, MT, in early 1990. This planning spawned the notion that it was time that we started doing a better job of collaborating between colleagues in Europe, Asia, and North America. The logical starting point was an international workshop that addressed those items that held common interest for European, Asian, and North American specialists. So, the international planning transmission was put into gear and 2½ years later a workshop was held in St. Moritz, Switzerland.

The primary objectives of the Stone Pine Workshop were:

1. To improve international cooperation and collaboration between scientists.
2. To exchange research findings.
3. To determine knowledge gaps in the ecology and management of subalpine stone pines of the world.

All five subalpine stone pines were covered by authors of 48 papers from Europe, Asia, and North America. They were:

Species	Natural range
Swiss stone pine (<i>Pinus cembra</i>)	European Alps, Carpathian Mountains
Siberian stone pine (<i>Pinus sibirica</i>)	Siberian Russia and Northern Mongolia (95 percent in Russia, 5 percent in Mongolia)
Japanese stone pine (<i>Pinus pumila</i>)	Japan, Korea, Eastern Siberia
Korean stone pine (<i>Pinus koraiensis</i>)	Northeastern China, North Korea, Honshu Japan, southeastern Russia
Whitebark pine (<i>Pinus albicaulis</i>)	Western North America

The 12 countries represented and the number of papers from each country were: Russia (9), China (1), Japan (4), Switzerland (5), Austria (4), Italy (3), France (1), Yugoslavia (1), Czechoslovakia (1), Romania (1), Germany (3), and United States (15). The main subjects covered were:

- Evolution and taxonomy.
- Basic ecology of stone pine species.
- Growth characteristics.
- Influence of environmental factors.
- Regeneration.
- Importance to wildlife.
- Forest structure and dynamics.
- Forest management.
- Research needs.

Stone pines are critical forest components on vast areas. *Pinus sibirica* alone covers 40 million hectares, mainly in Siberia, and is a key component of the economy and biology. *P. koraiensis* accounts for one-fourth of the timber production in China. *P. albicaulis* is key to the survival of wildlife such as the grizzly bear and is a protector of high-elevation watersheds and visual resources. *P. cembra* plays a key role in avalanche protection, wood production, and recreation in Europe. *P. pumila* is a key high-elevation species for stabilization of mountain slopes in Japan and Kamchatka. These species have many things in common, likely starting with a common ancestor, probably *P. sibirica*. They also share common methods of seed dispersal with the North American and Eurasian nutcrackers. Natural selection processes have resulted in a real mutualism between subalpine stone pines and the nutcrackers.

This workshop was sponsored by the Intermountain Research Station, USDA Forest Service, U.S.A.; the Westfälische Wilhelms-Universität, Landscape Ecology Division, Germany; the Swiss Federal Institute for Forest, Snow, and Landscape Research, Switzerland; and the Karl and Sophie Binding Foundation, Switzerland.

We want to acknowledge the people and the organizations that supported them for their enthusiastic and dedicated efforts in the planning and conduct of this international workshop. Three field tours were conducted by the hosts of the workshop. The first tour entitled "Engadine Cembra Pine-Larch Forest," was in a cembra pine-larch forest overlooking St. Moritz, a heavily used recreation area in the Engadine. The primary subjects were tree regeneration and succession in avalanche tracks and, at the upper timberline, squirrel and nutcracker interactions, human historical influence, grazing and game, and the pressures of modern tourism on the forests and landscape.

The second tour, entitled "Ecology and Technique of High-Altitude Afforestation," dealt primarily with management of avalanche-prone areas. It was conducted in the Stillberg Experimental Area near timberline in the Dischma Valley near Davos. It demonstrated the use and design of physical barriers for avalanche control and reforestation methods with cembra pine, larch, and mugo pine for long-term reduction of avalanche problems.

The third tour, entitled "Subalpine and Alpine Environments," emphasized vegetation succession, particularly of cembra pine and larch following the gradual retreat of the Morteratsch Glacier. Also included in this tour was a visit to the glacier areas at Diavolezza on the Bernina Pass where recreation values are paramount. From the aerial tram to the

mountain station (2,973 m) we viewed the strong contrasts of vegetation and glaciers on the north slopes of the Bernina Pass area.

For all the hosts of the enlightening field tours and arrangements at St. Moritz we owe a special thanks. Those included Drs. W. Schönenberger, R. Häslar, J. Senn, R. Lässig, F.-K. Holtmeier, and Herr U. Wasem—also Engadine Foresters J. Altman, I. A. Bisaz, and G. Bott. We also thank Prof. Dr. H. Steinlin from the Binding-Siftung who attended the workshop as representative of the Binding Foundation. All of these people and their staffs were wonderful hosts who contributed so much to the success of this first international conference on stone pines.

A special thanks goes to Kathy McDonald, Intermountain Research Station, U.S.A., who processed all the manuscripts.

The organizing committee was composed of the following people:

Dr. W. Schönenberger
Dr. R. Häslar
Dr. J. Senn
Swiss Federal Institute for
Forest, Snow and Landscape Research
Zurcher Str. 111
CH-8903 Birmensdorf
Switzerland

Prof. Dr. F.-K. Holtmeier
University of Munster
Department of Geography
Landscape Ecology Division
Robert-Koch-Str. 26
W-4400 Munster
Germany

Dr. Wyman C. Schmidt
USDA Forest Service
Intermountain Research Station
Forestry Sciences Laboratory
Montana State University
Bozeman, MT, 59717-0278, U.S.A.

Drs. Holtmeier and Schmidt served as technical evaluators of all the papers.

As a consequence of this international workshop, a resolution was passed by the scientists in attendance that aimed toward greater coordination and sharing of research findings. The resolution was:

1. To organize an International Association for Stone Pine Research.
2. To form an international organizing committee by election that could probably meet in Tomsk, Russia, in 1993 (or later) to (a) establish the objectives of the Association; and (b) establish the organizational structure of the Association.
3. The organizing committee to develop the preliminary plan for the next International Stone Pine Workshop.
4. To hold the next International Stone Pine Workshop at Tomsk, Russia, in 1995 (or later).

The world faces many environmental and resource challenges. Many of these challenges are in temperate forests of the Northern Hemisphere. In these, stone pines are a significant forest component and one in which our knowledge base is certainly not complete. Sharing the knowledge developed from similar ecosystems and building on that solid base is key to a better understanding of how our subalpine forests function ecologically. We can learn much from each other. The international workshop that generated this proceedings is a good first step in that direction. Let us do what we can together to keep the momentum.

Wyman C. Schmidt

F.-Karl Holtmeier

VORWORT

Dieser Band ist eine erste umfassende internationale Studie über die subalpinen Steinkiefern der Erde. Er enthält die Vorträge, die anlässlich des Internationalen Workshops "Subalpine Stone Pines and Their Environment—The Status of Our Knowledge" gehalten wurden. Dieser Workshop fand vom 5. bis 11. September 1992 in St. Moritz (Schweiz) statt. Die fünf subalpinen Steinkieferarten sind ausschließlich in der Nordhemisphäre verbreitet—davon eine in Nordamerika und vier in Eurasien. Diese Arten weisen viele gemeinsame Merkmale auf und besetzen auch ähnliche ökologische Nischen. Unter Steinkiefern versteht man die Arten des Genus *Pinus* mit fünfnadeligen Kurztrieben, flügellosen Samen und Zapfen, die im Reifezustand geschlossen bleiben.

Die Vorgeschichte dieses Internationalen Workshops beginnt 1987. Damals fand in Bozeman ein Workshop über die Whitebark Pine (*Pinus albicaulis*) statt, dem 1989 ein großes Symposium, ebenfalls in Bozeman, folgte. Beide Veranstaltungen stießen auf eine große Resonanz und führten zu einem wachsenden Interesse an den Hochgebirgsökosystemen des westlichen Nordamerika. Eine Vortragssektion dieses Symposiums war den Hochgebirgsökosystemen der Welt gewidmet. Dabei zeigte sich, daß aus einem Vergleich mit Steinkiefer-Ökosystemen anderer in ihrer Naturlandschaft mit dem nordamerikanischen Verbreitungsareal der Whitebark Pine vergleichbarer Regionen der Erde auch wichtige Informationen zum besseren Verständnis der Whitebark Pine - Wälder gewonnen werden können. Als ein wesentlicher Unterschied zu den amerikanischen Whitebark Pine - Wäldern erwies sich die zum Teil schon einige tausend Jahren zurückreichende anthropogene Beeinflussung der eurasiatischen Steinkiefernwälder durch den Menschen. Mit Sicherheit lassen sich aus den dortigen Verhältnissen auch nützliche Hinweise auch potentielle Auswirkungen menschlicher Eingriffe in den amerikanischen Whitebark Pine - Wäldern gewinnen.

Anfang 1990 traf sich dann eine kleine Gruppe von Wissenschaftlern und Forstleuten aus den westlichen Vereinigten Staaten mit Dr. Holtmeier (Münster, Deutschland) in Missoula (Montana), um über weiterführende Forschungen über die subalpinen Steinkiefern zu beraten. Der nächste Schritt sollte eine Verbesserung und Intensivierung der wissenschaftlichen Zusammenarbeit der Fachleute aus Europa, Asien und Nordamerika sein. Man kam überein, ein Internationalen Workshop zu veranstalten, mit dem Ziel, dort Fragen von gemeinsamem Interesse zu diskutieren und neue Forschungsansätze zu entwickeln. Unmittelbar nach diesem Treffen begannen die Vorbereitungen zu diesem Workshop, der dann zweieinhalb Jahre später in St. Moritz (Schweiz) stattfand.

Seine Hauptziele waren:

1. Verbesserung und Intensivierung der internationalen Zusammenarbeit.
2. Austausch von Forschungsergebnissen.
3. Forschungsbedarf hinsichtlich der Ökologie und Bewirtschaftung subalpiner Steinkiefernwälder aufzuzeigen.

Über alle fünf Steinkieferarten wurden Vorträge gehalten. Insgesamt waren es 48 Referate, an denen Wissenschaftler aus 12 Staaten beteiligt waren.

Bei den Arten handelte es sich um:

Art	Natürliches Verbreitungsgebiet
Arve (Synonym: Zirbe) (<i>Pinus cembra</i>)	Europäische Alpen, Karpaten
Sibirische Arve (<i>Pinus sibirica</i>)	Russisch Sibirien und nördliche Mongolei (95 percent in Rußland; 5 percent in der Mongolei)
Sibirische Zwergarve (Japanische Steinkiefer) (<i>Pinus pumila</i>)	Japan, Korea, Ostsibirien
Koreanische Steinkiefer (<i>Pinus koraiensis</i>)	Nordost-China, Nordkorea, Honshu, Südostasien
Weißrinden-Kiefer (<i>Pinus albicaulis</i>)	Westliches Nordamerika

Folgende Länder waren vertreten (Zahl der Beiträge in Klammern): Rußland (9), China (1), Japan (4), Schweiz (5), Österreich (4), Italien (3), Frankreich (1), Jugoslawien (1), Tschechoslowakei (1), Rumänien (1), Deutschland (3) und USA (15)

Die Hauptthemen waren:

- Evolution und Taxonomie.
- Autökologie der subalpinen Steinkieferarten.
- Wachstumscharakteristik.
- Einfluß der Standortfaktoren.
- Regeneration.
- Bedeutung der Steinkiefern für die Tiere.
- Waldstrukturen und -dynamik.
- Waldbewirtschaftung und -pflege.
- Forschungsbedarf.

Die Steinkiefern stellen einen hohen Anteil an der Waldbedeckung großer Gebiete. Allein *Pinus sibirica* bedeckt ein Areal von 40 Millionen Hektar. Der größte Teil davon liegt in Sibirien, wo der Sibirischen Arve sowohl in ihrer Bedeutung für die Wirtschaft als auch im Hinblick auf die biologische Situation die Rolle eines Schlüsselfaktors zukommt. *Pinus koraiensis* stellt ein Viertel der Holzproduktion in China. *Pinus albicaulis* ist unter anderem für den Grizzly-Bär von existentieller Bedeutung. Außerdem erfüllt diese Art in hochgelegenen Wassereinzugsgebieten eine wichtige Schutzfunktion und erhöht zudem wesentlich den ästhetischen Reiz der Gebirgslandschaft. *Pinus cembra* kommt in Europa eine wichtige Rolle bei der Lawinenvorbeugung durch Schutzwälder zu. Zugleich liefert sie ein für Täfeln und Schnitzereien geschätztes Holz. Auch sie ist von hohem ästhetischen Wert. *Pinus pumila* trägt in Japan und Kamtschatka entscheidend zur Stabilisierung steiler Gebirgshänge bei. Die vielen Gemeinsamkeiten der genannten Arten haben ihre Ursache vermutlich in ihrer Abstammung von einer Art, möglicherweise von *Pinus sibirica*. Charakteristisch ist für sie auch die Verbreitung ihrer Samen durch den nordamerikanischen und europäischen Tannenhäher. Zwischen den subalpinen Steinkiefern und den Hähern hat sich im Laufe der Evolution ein echter Mutualismus entwickelt.

Der Workshop wurde unterstützt durch die Intermountain Research Station, USDA Forest Service, USA, die Westfälische Wilhelms-Universität (Münster, Deutschland), die Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft (Schweiz) sowie durch die Karl und Sophie Binding - Stiftung.

Wir danken allen Personen und Organisationen, die mit ihrem Enthusiasmus und ihrer tatkräftigen Unterstützung die Planung und die Durchführung dieses Workshops ermöglicht haben.

Während des Workshops fanden unter der Leitung der Gastgeber drei Exkursionen statt. Die erste führte in die Lärchen-Arvenwälder oberhalb des bekannten Engadiner Höhenkurortes St. Moritz. Hauptthemen waren die Verjüngung und Sukzession in Lawinenzügen und im Waldgrenzbereich, die Einbindung von Eichhörnchen und Tannenhäher in das Ökosystem des Lärchen-Arvenwaldes, die Einflüsse von Beweidung und Wild sowie die Belastungen der Wälder und der Landschaft durch den modernen Tourismus.

Die zweite Exkursion, die sich im wesentlichen mit ökologischen Problemen und Techniken bei der Hochlagenaufforstung und der Behandlung von Lawineneinzugsgebieten befaßte, führte in die im Waldgrenzbereich gelegenen Versuchsflächen am Stillberg im Dischmatal bei Davos. Dort wurden künstliche Lawinenverbauungen und Wiederaufforstungen mit Arven, Lärche und Legföhre als Mittel zur Lawinenvorbeugung demonstriert.

Die dritte Tour, die unter dem Thema "subalpine und alpine Lebensräume" stand, führte zunächst in das Morteratsch-Tal. Dort ging es vor allem um die Vegetationssukzession im Vorfeld des allmählich zurückweichenden Morteratsch-Gletschers unter besonderer Berücksichtigung der Besiedlung durch Arve und Lärche. Mit einem Besuch der Diavolezza am Berninapaf fand die Exkursion ihren Abschluß. Von der Bergstation (2973 m) der Luftseilbahn bot sich ein überwältigender Blick auf die stark vergletscherte Nordseite der Berninagruppe.

Für alles, die erlebnisreichen und lehrreichen Exkursionen sowie die Veranstaltungen in St. Moritz, schulden wir den Gastgebern — Drs. W. Schönenberger, R. Häsler, J. Senn, R. Lässig, F.-K. Holtmeier und Herr U. Wasem — sowie den Engadiner Förstern J. Altmann, I.A. Bisaz, und G. Bott besonderen Dank. Nicht zuletzt geht unser Dank auch an Herrn Prof. Dr. H. Steinlin, der als Vertreter der Binding-Stiftung selbst an dem Workshop teilnahm. Sie alle haben mit ihrem großen Engagement bei der Planung und der Durchführung zum Gelingen dieses ersten internationalen Workshops über die Steinkiefern beigetragen.

Besonderer Dank gilt auch Frau Kathy McDonald und Herrn Richard Klade (Intermountain Research Station, USA) für die redaktionelle Bearbeitung der Manuskripte.

Das Organisationskomitee setzte sich zusammen aus:

Dr. W. Schönenberger
Dr. W. Häsler
Dr. J. Senn
Eidgenössische Forschungsanstalt
für Wald, Schnee und Landschaft
Zürcher Straße 111
CH-8093 Birmensdorf
Schweiz

Prof. Dr. F.-K. Holtmeier
Westfälische Wilhelms-Universität
Institut für Geographie
Abteilung Landschaftsökologie
Robert-Koch-Straße 29
D-48149 Münster
Deutschland

Dr. Wyman C. Schmidt
USDA Forest Service
Intermountain Research Station
Forestry Sciences Laboratory
Montana State University
Bozeman, Montana, USA 59717-0278

Die Vorbereitung der Manuskripte für die redaktionelle Bearbeitung wurde von Dr. Holtmeier und Dr. Schmidt durchgeführt.

Während des Workshops veranschiedeten die Teilnehmer eine Resolution, die eine noch weitergehende Koordination der Forschung und bessere gegenseitige Information über neue Forschungsergebnisse zum Ziel hat. Sie umfaßt folgende Punkte:

1. Gründung einer Internationalen Vereinigung für die Erforschung der Steinkiefern.
2. Bildung eines Internationalen Organisationskomitees, das erstmals 1993 (oder später) in Tomsk (Rußland) zusammentreten soll, um die künftigen Ziele dieser Vereinigung zu formulieren und eine Organisationsstruktur zu schaffen.
3. Planung des nächsten Internationalen Workshops über die Steinkiefern.
4. Durchführung dieses Workshops voraussichtlich 1995 (oder später) in Tomsk.

Die Welt sieht sich vielen Herausforderungen durch Umweltprobleme und Ressourcennutzung gegenüber. Davon sind auch die Gebirgswälder und borealen Wälder der Nordhemisphäre betroffen, zu denen auch die Steinkiefernwälder gehören. Das Wissen über sie ist noch lückenhaft. Indem wir unser Wissen zusammentragen bilden wir eine solide Grundlage, von der aus es leichter sein wird, tiefere Einsichten in die ökologischen Wirkungsgefüge dieser Waldökosysteme zu gewinnen. Der Internationale Workshop in St. Moritz mit den hier zusammengestellten Beiträgen ist ein erster Schritt in diese Richtung. Jetzt geht es darum, diesen Weg weiterzugehen.

Wyman C. Schmidt

F.-Karl Holtmeier

CONTENTS

AUTHORS	TITLE	PAGE
Wyman C. Schmidt	Distribution of Stone Pines	1
FIELD TOURS		
Swiss Hosts Mihailo Grbic	Tour Descriptions	8
Friedrich-Karl Holtmeier	Introduction to the Upper Engadine and Its Forest	9
EVOLUTION AND TAXONOMY		
Konstantin V. Krutovskii Dmitri V. Politov Yuri P. Altukhov	Genetic Differentiation and Phylogeny of Stone Pine Species Based on Isozyme Loci	19
Hermann Mattes	Coevolutional Aspects of Stone Pines and Nutcrackers	31
Dmitri V. Politov Konstantin V. Krutovskii	Allozyme Polymorphism, Heterozygosity, and Mating System of Stone Pines	36
Diana F. Tomback William S. F. Schuster	Genetic Population Structure and Growth Form Distribution in Bird-Dispersed Pines	43
BASIC ECOLOGY		
Ernst Frehner Walter Schönenberger	Experiences With Reproduction of Cembra Pine	52
P. L. Gorchakovsky	Distribution and Ecology of Siberian Stone Pine in the Urals	56
Rudolf Häsler	Ecophysiological Investigations on Cembran Pine at Timberline in the Alps, An Overview	61
Peter A. Khomentovsky	A Pattern of <i>Pinus pumila</i> Seed Production Ecology in the Mountains of Central Kamtchatka	67
Takayoshi Koike Rudolf Häsler Hans Item	Needle Longevity and Photosynthetic Performance in Cembran Pine and Norway Spruce Growing on the North- and East-Facing Slopes at the Timberline of Stillberg in the Swiss Alps	78
Luo Ju Chun	The Broad-leaved Korean Pine Forest in China	81
Tad Weaver	Climates Where Stone Pines Grow, A Comparison	85
GROWTH CHARACTERISTICS		
Kurt Holzer	Growth of Swiss Stone Pines That Originated From and Were Planted at Several Altitudes in the Austrian Alps	91
Takuya Kajimoto	Seasonal Patterns of Growth and Photosynthetic Activity of <i>Pinus pumila</i> Growing on the Kiso Mountain Range, Central Japan	93
Herbert Kronfuss	Height Growth in Cembran Pine as a Factor of Air Temperature	99
Josef Senn Walter Schönenberg Ueli Wasem	Survival and Growth of Planted Cembran Pines at the Alpine Timberline	105

INFLUENCE OF ENVIRONMENTAL FACTORS

Mihailo Grbic	Changes of Swiss Stone Pine Aphid Life Cycle, Density, and Population Structure in High-Altitude Swiss Stone Pine Afforestation	111
Raymond J. Hoff Susan K. Hagle Richard G. Krebill	Genetic Consequences and Research Challenges of Blister Rust in Whitebark Pine Forests	118
Karel Kaňák	Performance of <i>Pinus cembra</i> , <i>P. peuce</i> , and <i>P. strobiformis</i> Within Air-Polluted Areas	127
Todd Kipfer Katherine Hansen Ward McCaughey	Competition and Crown Characteristics of Whitebark Pine Following Logging in Montana, U.S.A.	130
Penelope Morgan Stephen C. Bunting Robert E. Keane Stephen F. Arno	Fire Ecology of Whitebark Pine Forests of the Northern Rocky Mountains, U.S.A.	136
Tad Weaver	Vegetation Distribution and Production in Rocky Mountain Climates—With Emphasis on Whitebark Pine	142

REGENERATION

I. Blada N. Popescu	Variation in Size and Weight of Cones and Seeds in Four Natural Populations of Carpathian Stone Pine	154
Mitsuhiro Hayashida	Role of Nutcrackers on Seed Dispersal and Establishment of <i>Pinus pumila</i> and <i>P. pentaphylla</i>	159
Harry E. Hutchins	Role of Various Animals in Dispersal and Establishment of Whitebark Pine in the Rocky Mountains, U.S.A.	163
Hermann Mattes	Size of Pine Areas in Relation to Seed Dispersal	172
Ward W. McCaughey	The Regeneration Process of Whitebark Pine	179
Ikuko Nakashinden	Japanese Stone Pine Cone Production Estimated From Cone Scars, Mount Kisokomagatake, Central Japanese Alps	188
Diana F. Tomback	Effects of Seed Dispersal by Clark's Nutcracker on Early Postfire Regeneration of Whitebark Pine	193
Vladislav N. Vorobjev	New Trend in Dendrochronology: 1. Theoretical Principles of Reprochronology	199
V. N. Vorobjev S. N. Goroshkevich D. A. Savchuk	New Trend in Dendrochronology: 2. Method of Retrospective Study of Semiference Dynamics in Pinaceae	201

IMPORTANCE TO WILDLIFE

Ronaid M. Lanner Barrie K. Gilbert	Nutritive Value of Whitebark Pine Seeds, and the Question of Their Variable Dormancy	206
David J. Mattson Daniel P. Reinhart	Bear Use of Whitebark Pine Seeds in North America	212
Diana F. Tomback	Ecological Relationship Between Clark's Nutcracker and Four Wingless-Seed <i>Strobos</i> Pines of Western North America	221

FOREST STRUCTURE AND DYNAMICS

Giovanna De Mas Elena Piutti	Structure of Swiss Stone Pine Stands in Northeastern Italy	226
S. Yu. Grishin	Role of <i>Pinus pumila</i> in Primary Succession on the Lava Flows of Volcanoes of Kamchatka	240
Robert E. Keane Penelope Morgan	Decline of Whitebark Pine in the Bob Marshall Wilderness Complex of Montana, U.S.A.	245
Renzo Motta Alberto Dotta	Some Aspects of Cembran Pine Regeneration in the Italian Cottian Alps	254
Pietro Piussi	Mixed Cembran Pine Stands on the Southern Slope of the Eastern Alps	261
Siegfried Sauermoser	Current Distribution of Cembra Pine in the Lechtal Alps	269
E. P. Smolonogov	Geographical Differentiation and Dynamics of Siberian Stone Pine Forests in Eurasia	275
Lise Wlérick	The Cembran Pine in the French Alps: Stand Dynamics of a Cembran Pine Forest in Tueda (Savoy, France)	280

FOREST MANAGEMENT

Werner Frey	Silvicultural Treatment and Avalanche Protection of Swiss Stone Pine Forests	290
Riet Gordon	Importance and Silvicultural Treatment of Stone Pine in the Upper Engadine (Grisons)	294
Jörg Heumader	Cultivation of Cembran Pine Plants for High-Elevation Afforestations	298
Katherine C. Kendall	Whitebark Pine Conservation in North American National Parks	302

RESEARCH NEEDS

Wyman C. Schmidt	Research Needs in Whitebark Pine Ecosystems	309
Vladislav N. Vorobjev Nina A. Vorobjeva	Problems of Comprehensive Investigation, Utilization, and Reproduction of Russian Cedar Pine Forests	314

DISTRIBUTION OF STONE PINES

Wyman C. Schmidt

The five stone pine species that are the subject of this proceedings occur only in the Northern Hemisphere—one species in North America and the other four in Europe and Asia. Taxonomically they fall in section *Strobus* and subsection *Cembrae*. They are characterized by having five-needled fascicles, cones that do not open at maturity, and seeds that are wingless.

The distributions of the five species are reasonably well defined, but updates on their distribution usually show minor changes. Also, in some cases, such as with whitebark pine (*Pinus albicaulis*), the species occurs only at high-elevation sites, and there may be long distances between the mountain ranges that support this species. This species occurs over a large geographic area; however, there are usually large intervening valleys and lowlands not suitable for whitebark pine forests. The same is true for the other stone pines. Therefore, just because a distribution boundary of a species encompasses a large area, it does not mean that all the mountains and valleys are fully occupied by that species.

For the purposes of this proceedings, we have chosen to show the general distribution on the maps of the five species and do not necessarily include all of the individual outliers.

The distribution maps that follow are adapted from those published by Critchfield and Little (1966). The maps show that the five species are mostly discrete populations, but there are overlapping distributions of Siberian stone pine (*Pinus sibirica*) and Japanese stone pine (*P. pumila*), and an overlap of Japanese stone pine and Korean stone pine (*P. koraiensis*).

Whitebark pine occurs only in North America at high elevations from central British Columbia south through the Cascade Mountains of Washington and Oregon to the southern Sierra Nevada of California, in a limited area of Nevada, and extensively in Montana, Idaho, and western Wyoming. It occurs just below the timberline and extends downward elevationally into associations with several other conifers.

Swiss stone pine grows at high elevations in the Alps and Carpathian Mountains. It occurs mostly in Switzerland, Austria, northern Italy, southeastern France, Romania, Czechoslovakia, and Poland. Although Swiss stone pine is considered closely related to Siberian stone pine, over 2,000 kilometers presently separate the two species.

Swiss stone pine commonly grows in association with other conifers.

Siberian stone pine is widely distributed in Eurasia from the Ural Mountains through western and central Siberia to northern Mongolia—an east-west distance of about 4,000 kilometers. It overlaps the range of Japanese stone pine on the eastern portion of its distribution near Lake Baikal in Siberia. Different than both whitebark pine and Swiss stone pine, which only occupy high-elevation sites, Siberian stone pine (usually called cedar-pine or Siberian cedar by Russians) commonly grows in the plains and river valleys, as well as in the mountain areas.

Japanese stone pine grows in northeastern Siberia and in subalpine parts of Japan, Korea, and Manchuria. It extends north almost to the Arctic Ocean (70° N.), west to Mongolia and to the Lake Baikal area, and south to Korea and Honshu, Japan. It grows from low elevations in the north to high elevations in the south. It commonly forms thickets just below barren tundra on tops of mountains or lowlands in the extreme north. Like Siberian stone pine, it extends nearly 4,000 kilometers from east to west and 3,000 kilometers north to south.

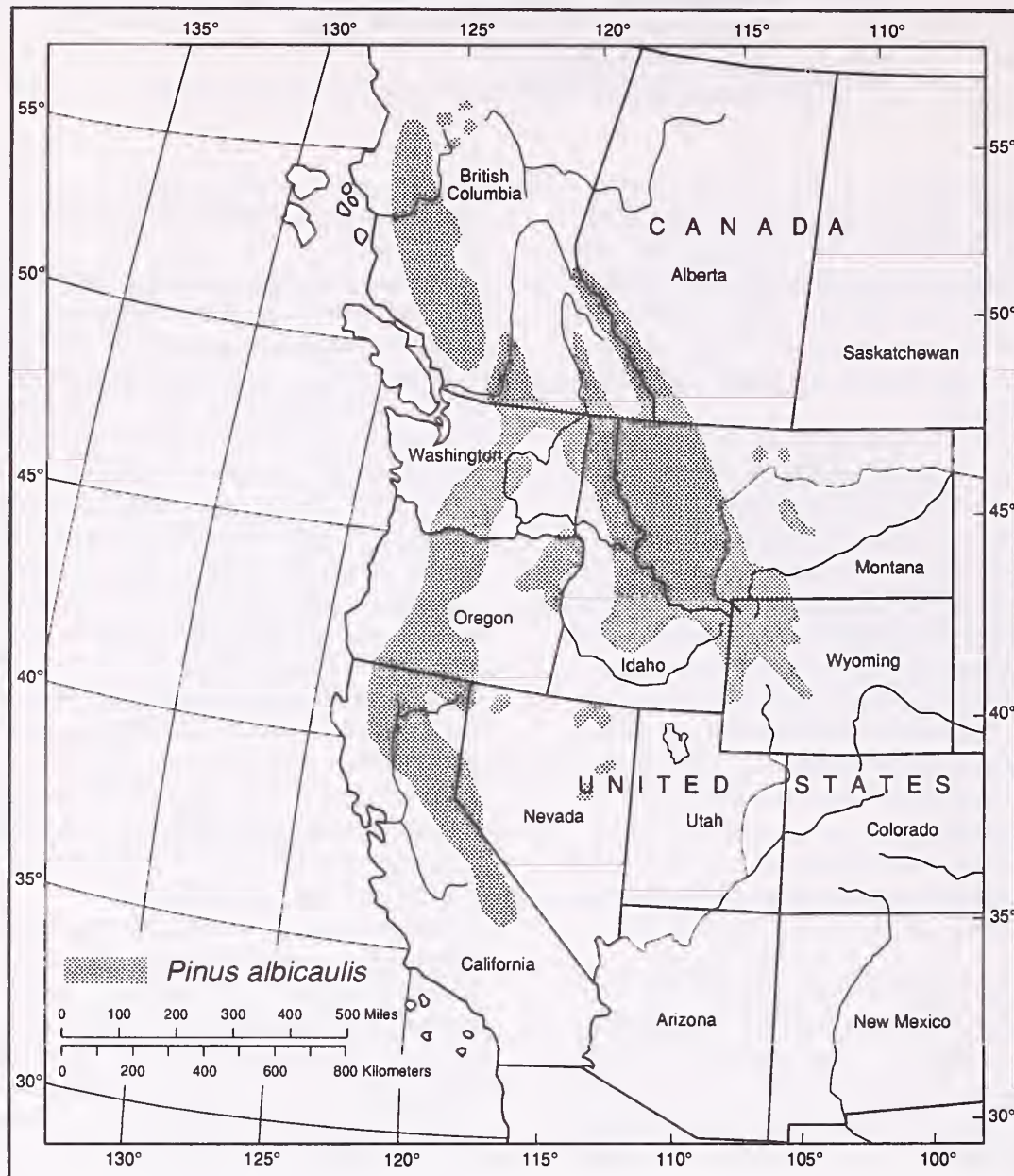
Korean stone pine occurs throughout Korea and eastern Manchuria into southeastern Siberia as well as on the islands of Honshu and Shikoku in Japan. It tends to grow in more maritime conditions and lower mountains than its neighbor—the Japanese stone pine. Its geographic range overlaps that of the Japanese stone pine, but the species occupy different ecological niches. Korean stone pine, unlike its counterparts, will grow in association with hardwoods where near-maritime climates prevail. Its valuable wood makes it a much sought after species.

The following maps illustrate the geographic distribution of the five stone pines. These descriptions are based primarily on those of Critchfield and Little (1966) and Mirov (1967).

References

- Critchfield, W. B.; Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Mirov, N. T. 1967. The genus *Pinus*. New York: Ronald Press Company. 602 p.

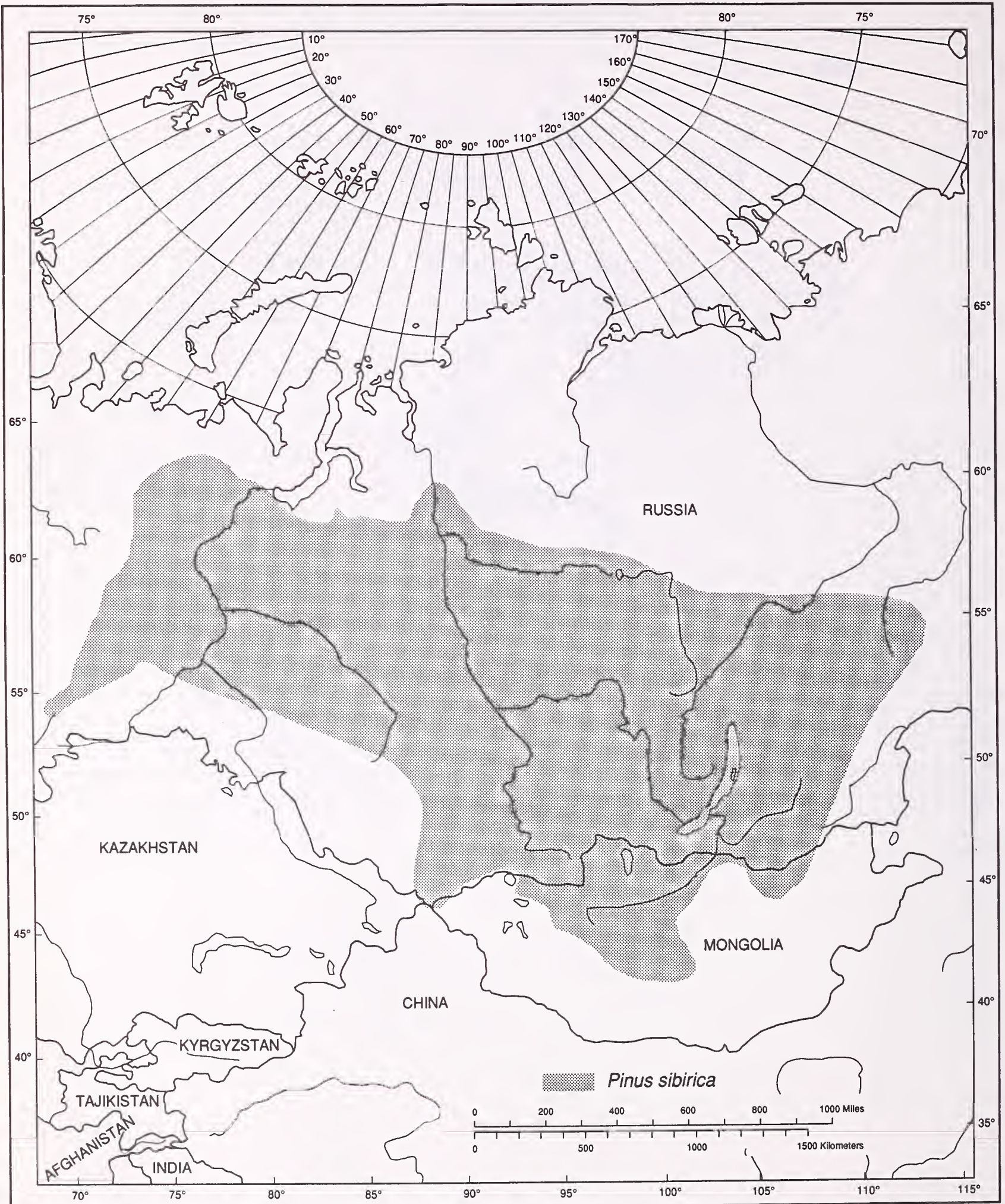
NORTH AMERICA



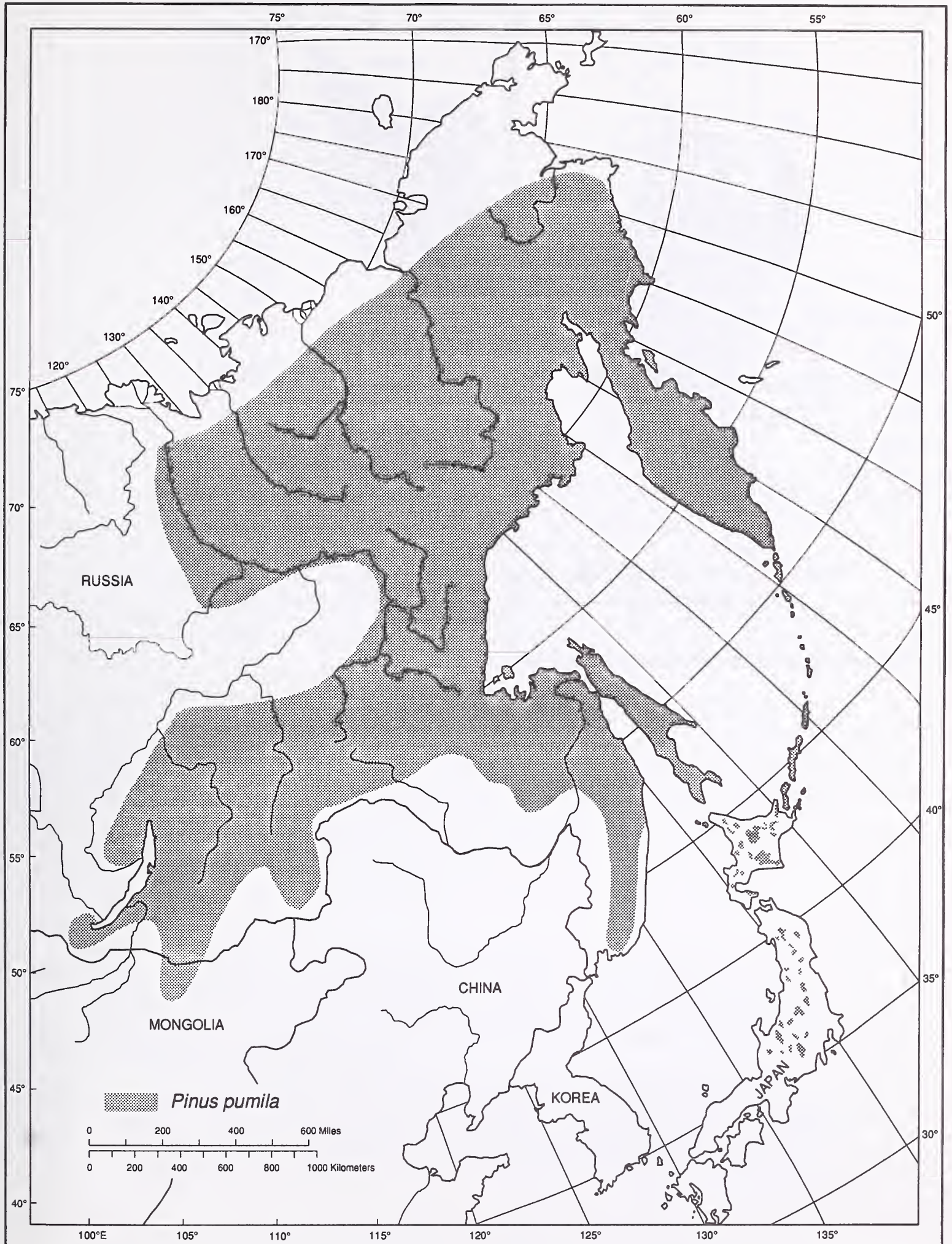
EUROPE



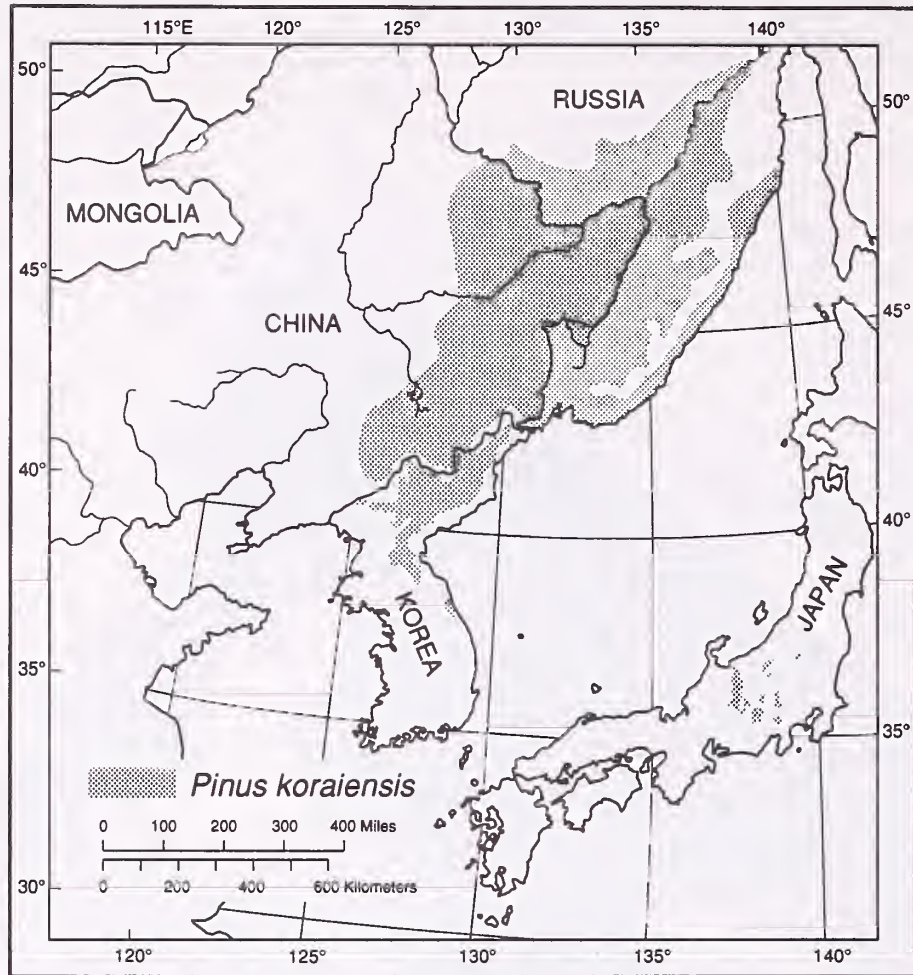
ASIA



ASIA



ASIA



Field Tours



International Workshop
St. Moritz 1992

Field tours were an important component of the Stone Pine Workshop. First, the tours provided an informal setting for scientists from the 12 countries to become acquainted with each other and their research; second, the tours demonstrated the research and management of Swiss stone pine forests in the rugged and spectacularly beautiful mountains of Switzerland.

The following section is the handout from the Swiss hosts used to describe the three major field tours. The drawings by a gifted scientist, Mihailo Grbic, from Belgrade, Yugoslavia, depict a symbolic participant, Dr. Stone Pine, enjoying the rather strenuous excursions. Grbic also created the welcome drawing used as sections division indicators in this publication.

TOUR DESCRIPTIONS

Swiss Hosts

We will try to use pleasant weather for the field tours. Therefore this preliminary schedule may change a little. Usually weather is fine in September. However, snow and frost are possible. Do not forget warm clothing, tough footwear, backpack, sunblock, and sunglasses. During the field tours we will have lunch from the backpack.

Engadine Cembra Pine-Larch Forest

Sunday 6th. St. Moritz, Muottas da Schlarigna. Walk from St. Moritz Bad (Hotel "Laudinella")-Stazer Wald-Muottas da Schlarigna-St. Moritz Bad (1,800 to 2,300 m above sea level [a.s.l.]).

Cembra pine-larch forest: composition, structure, growth characteristics, old cembra pines, regeneration pattern, understory vegetation, avalanche tracks with green alder (*Alnus viridis*) formation, influence of seed-caching animals (squirrel, nutcracker), effects of seed dispersal by the thick-billed European nutcracker (*Nucifraga c. caryocatactes*).

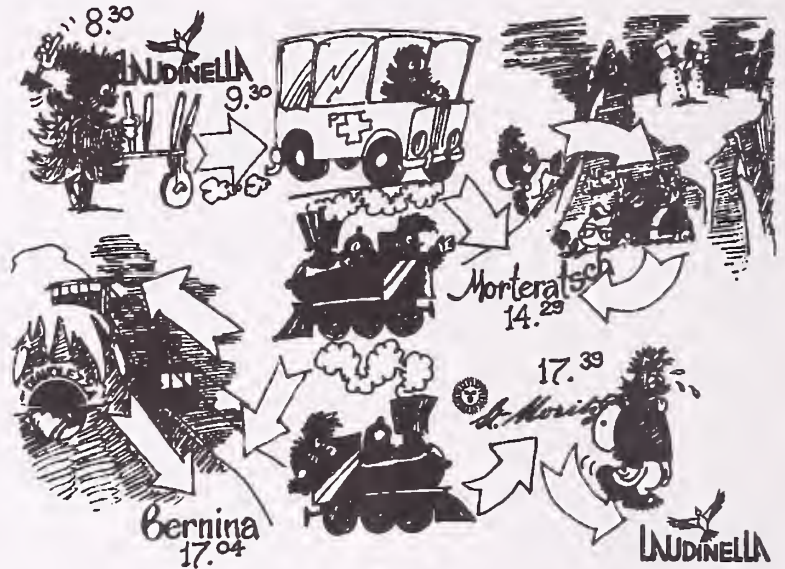
Human influence on the forest distribution pattern, human-caused timberline, influence of grazing livestock and game, and of tourism; invasion of rarely used and abandoned alpine and forest pastures by trees, influence of microtopography and microclimate on alpine vegetation and on growth of invading trees.

Ecology and Technique of High-Altitude Afforestation

Tuesday 8th. Davos, Stillberg. Bus from St. Moritz-Albula pass-Davos-Teufi (Dischma Valley, 1,700 m), 5-hour walk to and through Stillberg experimental area near timberline at 2,000 to 2,230 m a.s.l. and back to the valley bottom (Teufi).

The experimental area lies on a steep avalanche catchment slope. Construction of avalanche barriers. Damages, diseases, mortality and development of a 17-year-old

plantation of *Pinus cembra*, *Larix decidua*, and *P. mugo*. Influence of different site factors such as wind, temperature, irradiation, snow movement, duration of snow cover, soil properties, vegetation on plantation success. Eco-physiology of subalpine timberline trees. Conclusions for plantation technique and spatial patterns.



Subalpine and Alpine Environments

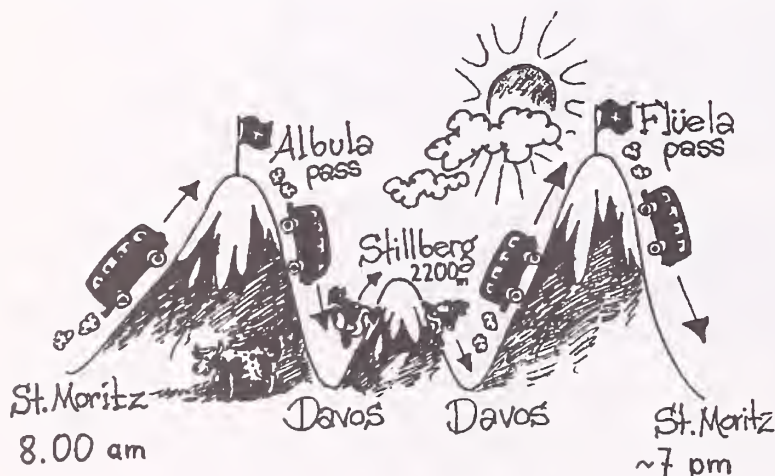
Friday 11th. Morteratsch Glacier, Diavolezza. Morteratsch Glacier (2,000 m, 2- to 3-hour walk). Train to Morteratsch station, walk to Morteratsch Glacier via Alp Chünetta (2,052 m); old-growth cembra pine forests, regeneration, invasion of the lateral moraine (from 1850) and the glacier forefield by cembra pine and larch.

Diavolezza (2,973 m). Train from Morteratsch station through the Bernina Valley to Diavolezza station (2,200 m) on Bernina Pass, and by ropeway to Diavolezza. Magnificent view of the Bernina Massive (4,049 m) with Pers Glacier and Morteratsch Glacier.

★★★★★

In addition to providing valuable scientific and management information, the introductory paper by Friedrich-Karl Holtmeier that follows gave background and baseline data describing the local Swiss stone pine forests that were the focus of the field tours.

★★★★★



INTRODUCTION TO THE UPPER ENGADINE AND ITS FOREST

Friedrich-Karl Holtmeier

Abstract—The Engadine is characterized by great mean elevation (2,400 m) and a relatively continental climate. Cembra pine (*Pinus cembra*) and European larch (*Larix decidua*) are the most important tree species. The area was already settled in prehistoric time. Since then, mountain forest has been influenced by human impact. During history timberline became lower by about 150-300 m. At present, the upper forest limit is located at about 2,200-2,300 m. Composition and structure of the forest also changed in that larch could spread at the cost of cembra pine on all areas that were suitable for grazing. After grazing pressure has declined natural succession is revived, and, in the long term, larch will be replaced by cembra pine, if not specially managed. Natural stands of Norway spruce (*Picea abies*) occur on the northwest-exposed slopes of the main valleys within an area characterized by higher humidity. Spruce reaches its upper limit at 2,000 m. Dwarfed mountain pine (*Pinus mugo*) and green alder (*Alnus viridis*) are most common in avalanche tracks. Green alder is to be found mainly on moist sites, whereas mountain pine prevails under dry conditions. Alder also occurs in bogs.

The Engadine—Engiadina in Rhaeto-Romanic languages—is located in the eastern part of Switzerland and comprises the uppermost drainage area of the Inn River (fig. 1). The main valley trends from southwest to northeast. By an administrative border the Engadine is divided into Upper and Lower Engadine. However, landscape physiognomy of both sections is also different. The Lower Engadine is deeply cut into the mountains, and mountain slopes are steep and rugged. The Upper Engadine main valley, on the other hand, is wide and topography is comparatively smooth. Between St. Moritz and the Maloja Pass the valley is characterized by four lakes separated by alluvial plains. To the southeast the Bernina Valley gives access to the famous glaciated Bernina Group.

The Engadine is characterized by great mean elevation (2,400 m). The bottom of the main valley is located at an altitude of about 1,800 m. The tributary valleys climb up to about 2,300 m. The highest peaks' elevations are about 4,000 m (Piz Bernina 4,049 m; fig. 1). In view of its great elevation the Upper Engadine has been called "The Roof of Europe" by the English.

Due to the geographical location in the central Alps and the high mass-elevation of the Engadine the climate is rather continental, characterized by a relatively great

amplitude of mean temperature and comparatively low amount of precipitation (fig. 2). Annual precipitation decreases from about 1,400 mm at Maloja Pass, where the main valley is open to moisture-carrying air currents from the southwest (fig. 3), to less than 1,000 mm at St. Moritz. At timberline, however, precipitation is much higher than at the valley bottom, as can be concluded from the data available for Julier Hospiz on Julier Pass and for Bernina Hospiz on Bernina Pass. At both stations, annual precipitation exceeds 1,500 mm.

Due to the continental climate, the upper limits of vegetation and cultivation reach relatively high altitudes. In the Upper Engadine, forest limit is located at about 2,200-2,300 m. Solitary crippled trees may still be found at and even above 2,500 m (Holtmeier 1965, 1974).

In the Upper Engadine, artifacts were found that give evidence of agriculture during the Bronze Age (about 3,000 years B.P.), while in the Lower Engadine hunters and shepherds were already present in the Neolithic Age (4,000 years ago; Conrad 1940). Trading and mining became increasingly important to the economy during historic time. Thus, there was increasing human impact on the mountain ecosystems throughout history. Almost no untouched nature was left, although the kind and the intensity of the human disturbances were different.

DEPRESSION OF TIMBERLINE

Due to the great elevation of the area humans could only use the mountains up to a certain altitude; there the

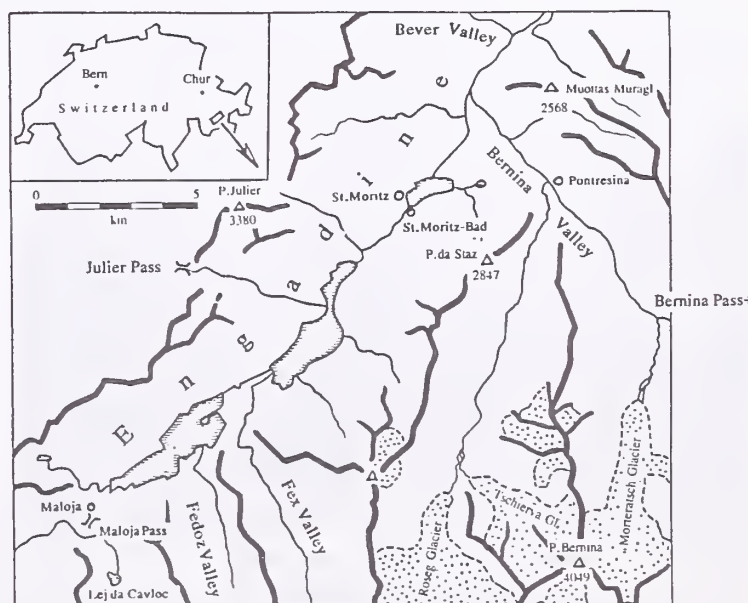


Figure 1—Location of the Upper Engadine.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Friedrich-Karl Holtmeier is Professor of Landscape Ecology and Geography, Department of Geography, University of Münster, Germany.

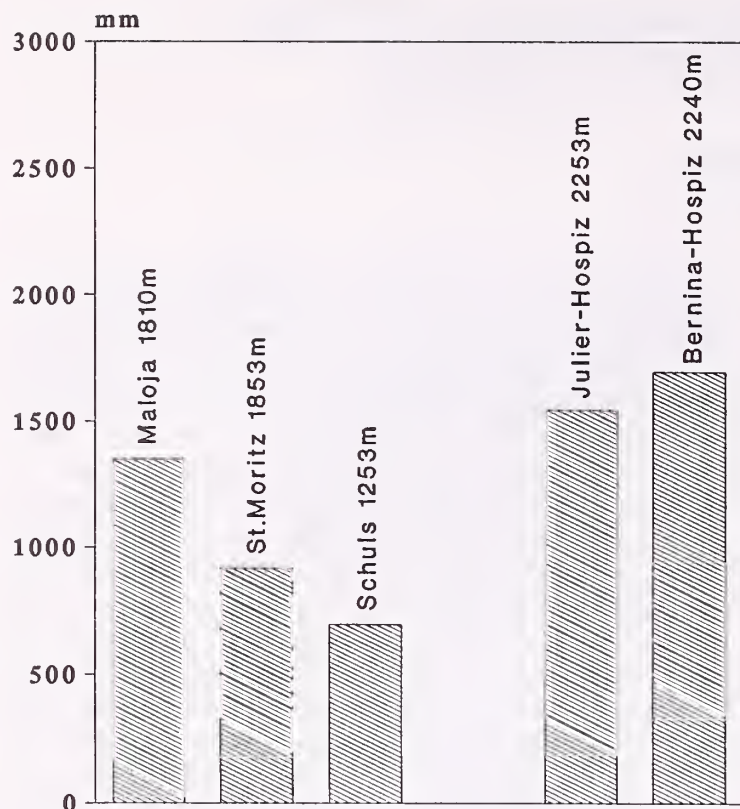


Figure 2—Annual precipitation. Note the decrease from Maloja Pass toward St. Moritz and Schuls (Lower Engadine).

main influence was concentrated in the forest belt not only on favorable southern exposures but also on all sections that were fairly accessible—trough shoulders, terraces, and similar almost-level areas even in north-exposed locations. During former times cereals were grown up to elevations of about 2,300 m, favorable topography provided. Many of the high-altitude forests were cleared for pastoral use, while those at lower elevations



Figure 3—View from Lejdals Chöds (northwest-facing slope of the main valley) southwest toward the gap of Maloja Pass.



Figure 4—Zuoz Village (1,700 m). The original forest was almost totally removed as a consequence of alpine pasturing (upper slope) and agriculture (artificial terraces above the village). Only two small stands were left on the steep north-exposed slopes of the narrow tributary valleys and one above the village for protection from avalanches. Photo taken 1968.

gave way to agriculture. The extent of timberline depression varied in relation to exposure and topography. On some easily accessible southern exposures of the main valley, for example, and of the Fex Valley and Fedoz Valley, the forest was totally removed except for sections characterized by too great steepness (figs. 4, 5). Other forests were destroyed by ore mining, salt works, and charcoal production, especially during the Middle Ages. On



Figure 5—View to southeast-exposed slope of the main valley. In the foreground, Samaden Village (1,720 m). Forest was removed from all gentle topography (trough shoulders, lower slope area) and reduced to a narrow belt on the steep trough wall. Photo taken 1969.



Figure 6—View from Diavolezza trail to Bernina Pass (2,328 m). Bernina Pass was covered by larch-cembra pine forest until the Middle Ages. Then, the forest became a victim of mining. Until present, the area is used in summer for grazing cattle.

the Bernina, Abula, and Julier Passes (about 2,300 m) the forest disappeared as a consequence of mining. These areas were then used as alpine pastures (fig. 6).

The upper timberline receded by 150-300 m compared to its position during the postglacial thermal optimum. That timberline depression was partly due to a general cooling. However, at least since the Middle Ages the effects of the deterioration of the climate on subalpine tree growth have been compounded or even superimposed by the human influences mentioned earlier.

COMPOSITION AND STRUCTURE

As a consequence of these activities not only did the upper timberline become lower by about 150-300 m, but also species composition and structures of the mountain forests changed considerably (Auer 1947; Campell 1944; Holtmeier 1965, 1967). Larch (*Larix decidua*) and cembra pine (*Pinus cembra*) are the most important tree species in the Upper Engadine forests. These forests belong to the so-called silicate type (*Larici Cembraetum*, Ellenberg 1978; *Larici-Pinetum cembrae*, Oberdorfer 1970) of larch-cembra pine forest, which is common in the crystalline Central Alps. The present distribution pattern of both species in the Upper Engadine can be described as follows: Cembra pine is mainly spread on steep and inaccessible slopes and north exposures, whereas larch dominates on easily accessible locations exposed to the south.

The influence of the local topography on the distribution pattern is most pronounced in the trough-shaped Bever Valley and Bernina Valley (fig. 7). Pure larch stands are confined to the relatively gentle slope areas (talus cones, screes, boulder fans, etc.) that extend below the steep and rocky trough walls, while cembra pine prevails on trough walls and also forms the upper timberline. This pattern is most conspicuous on southern exposures. On north-exposed slopes cembra pine also occurs on their lower parts, mixed with larch.

This distribution of larch and cembra pine is mainly caused by human influences, especially by pastoral use. Since cembra pine impedes the growth of grass and herbs on the forest floor, while larch does not, cembra pine was cleared on slopes suitable for grazing and restricted to steep, inaccessible locations. Moreover, the wood of cembra pine was used for many purposes such as paneling and making furniture, milk vessels, or carvings. Cembra pine also is more susceptible to forest fires than larch, which is protected by a thick corklike bark. As indicated by charcoal-rich soil horizons, forest fires frequently occurred in the past. Probably, many of them were caused by shepherds when they burned alpine pastures to remove "weeds" such as *Rhododendron ferrugineum* and *Juniperus nana*, and fires ran out of control. Thus, for many reasons, larch could spread at the cost of cembra pine, as was also the case in many other central-alpine valleys. At many places the high-elevation forest is over-mature and very sensitive to environmental impacts such as windthrow and snow slides.

CURRENT CHANGES

Due to modern change of economic structure—tourism has become the main base of the economy in the Engadine—grazing pressure on the forests declined, and cembra pine is invading the former pasture forest. Larch, which is a light-demanding species, is going to be out-competed by cembra pine, and natural succession from larch to cembra pine forests, which had been interrupted by human disturbances for some hundred years, is revived (Holtmeier 1967, 1990, 1993). Larch will gradually be replaced by cembra pine, if sites are not specially managed by exposing mineral soil or selective cutting of cembra pine.

Locally, however, invasion of cembra pine in the understory is hampered by mass outbreaks of the larch bud moth (*Zeiraphera diniana*). After having defoliated the larch crowns, the caterpillars will feed on the cembra pines in the understory and, together with secondary parasites, cause severe damage to them. Young cembra pines become crippled or killed.

In forest gaps smaller than the height of the surrounding trees, accumulation of snow and length of winter snow cover may critically increase (fig. 8), and consequently seedlings and saplings of cembra pine may be seriously damaged by snow fungus (*Phacidium infestans*).

Cembra pine also is invading abandoned or only rarely used alpine pastures. Seeds are dispersed by the nutcracker (*Nucifraga caryocatactes*), occasionally far beyond the present forest limit (Holtmeier 1966, 1974; Mattes 1978, 1982). Larch seeds, however, are prevented from getting into a suitable seedbed by the dense alpine vegetation. Thus, it is cembra pine that is the pioneer species on former pasture areas (fig. 9), while larch only occurs where bare mineral soil is exposed. Survival of the invading trees mainly depends on microclimates and resulting site conditions. They considerably deteriorated when the forest was removed in the past. Favorable effects of the general warming on tree growth are superimposed by unsuitable local site conditions (fig. 10). Consequently, natural reforestation follows the favorable sites while other sites will remain treeless probably for a long time.

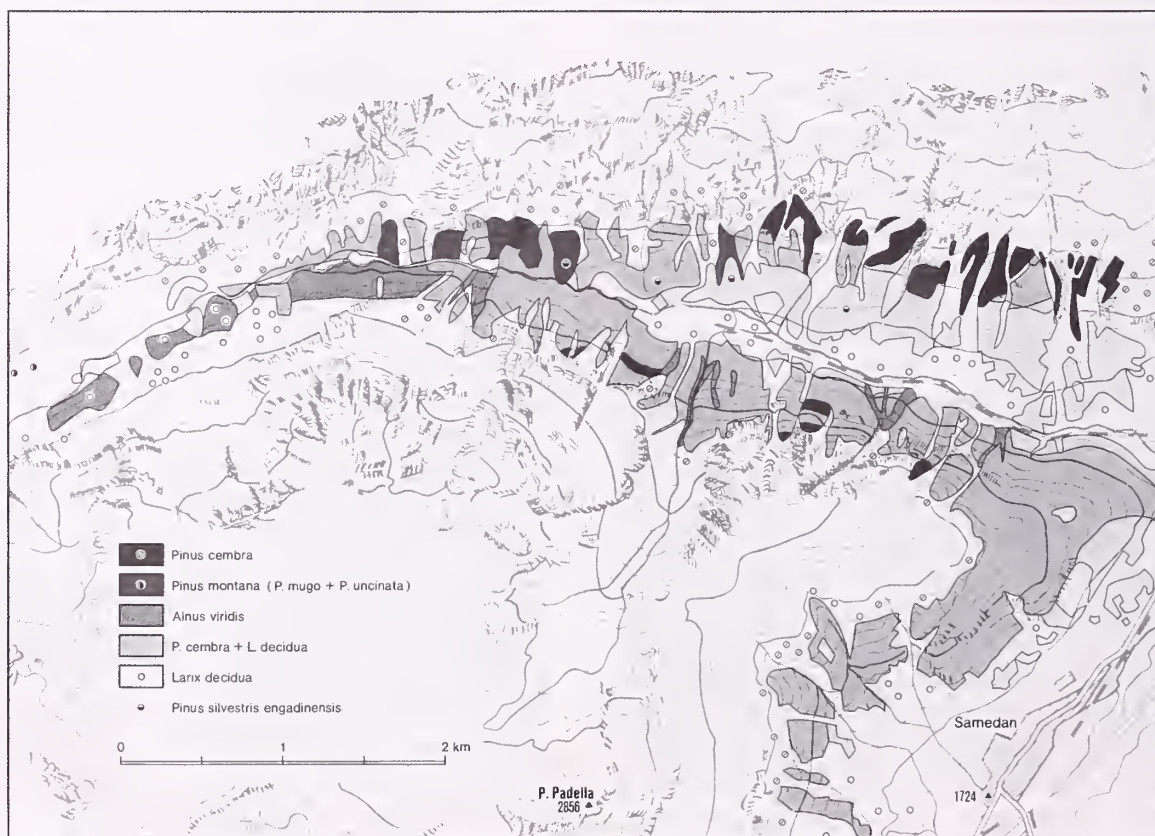
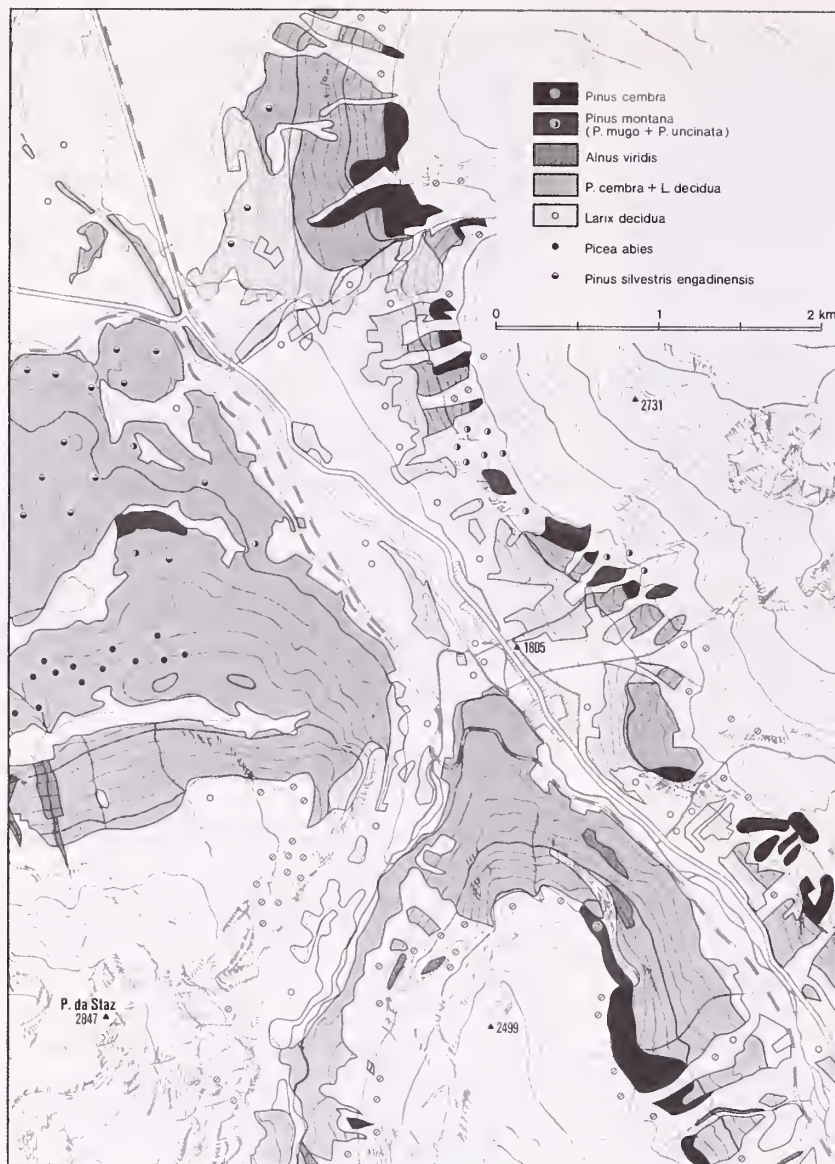


Figure 7—Distribution of tree species in the Bernina Valley (top) and Bever Valley (bottom). Both maps have been redrawn from Holtmeier (1967).

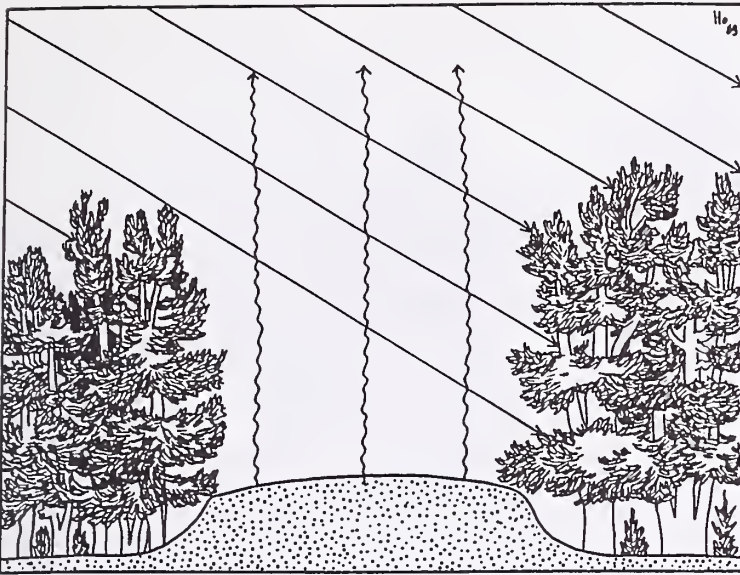
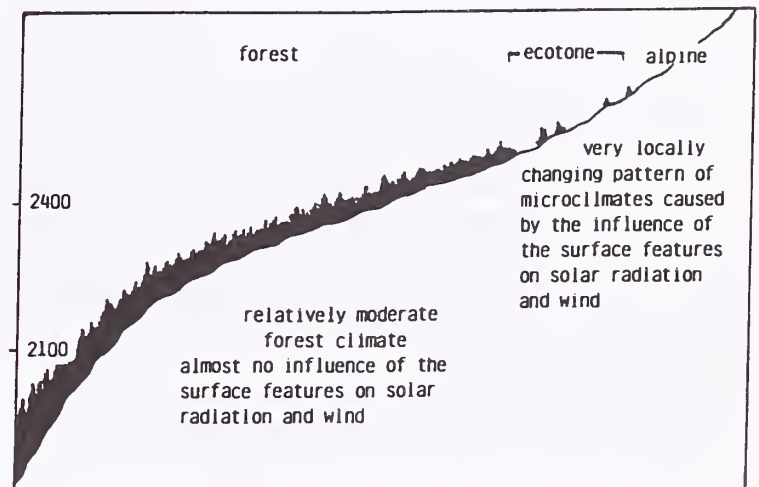


Figure 8—Big snow masses are accumulated in the glade. Incoming solar radiation is intercepted by the trees, while energy loss by outgoing long-wave radiation is almost unimpeded. Due to these conditions snowmelt is considerably delayed, and young cembra pines may be infected by snow fungus.

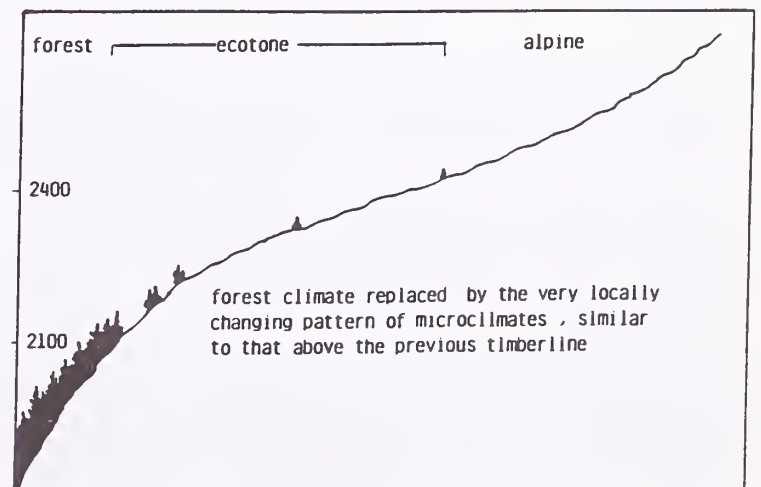
As to successful germination and survival of seedlings, seed dispersal by the nutcracker is much more effective than wind-mediated transport because many seeds are cached at sites relatively favorable to germination and seedling growth (not too long covered with snow). On the other hand, the seed caches usually provide sufficient soil moisture because they are 2-4 cm under the surface, thus being protected from direct insolation. Finally, seeds collected by the nutcracker are characterized by a relatively high germination capacity (Mattes 1978, 1982), and there is almost no loss of cached seeds by seed-eating predators.

However, due to high density of seedling clusters some of the trees will become victims of root competition. Moreover, snow accumulation and duration of the snow cover may gradually be increased by the influence of the growing trees on windflow near the surface. At such sites, young cembra pines covered too long by snow may be killed by snow fungi such as *Phacidium infestans* (Holtmeier 1967, 1974, 1990).

Natural invasion by trees (cembra pine, larch, willows, rowan, and also spruce) can be observed in front of and on the lateral moraines of the Morteratsch Glacier and Roseg Glacier (Holtmeier 1965, 1974, 1990; fig. 11). These glaciers have been retreating more or less continuously by about 30 m per year since the beginning of our century. Larch already occurs about 20 years after glacier retreat, while cembra pine will follow later. Then, however, cembra pine invades these areas much more rapidly than larch. There is some evidence that areas which became ice-free about 50 to 70 years ago were more rapidly invaded by cembra pine than those from where the glacier retreated more than 100 years ago. That might be explained by mesoclimatic conditions improving due to glacier retreat.



1. Situation during the postglacial thermal optimum



2. Situation at present



Figure 9—Cembra pine invading an abandoned alpine pasture (about 2,250 m) on the northwest-exposed slope of the main valley. Invasion follows mainly convex topography, while sites covered too long with snow and characterized by snow creep and avalanches remain treeless.

Figure 10—Change of microclimatic conditions in the upper Subalpine after the uppermost forest was removed by humans.

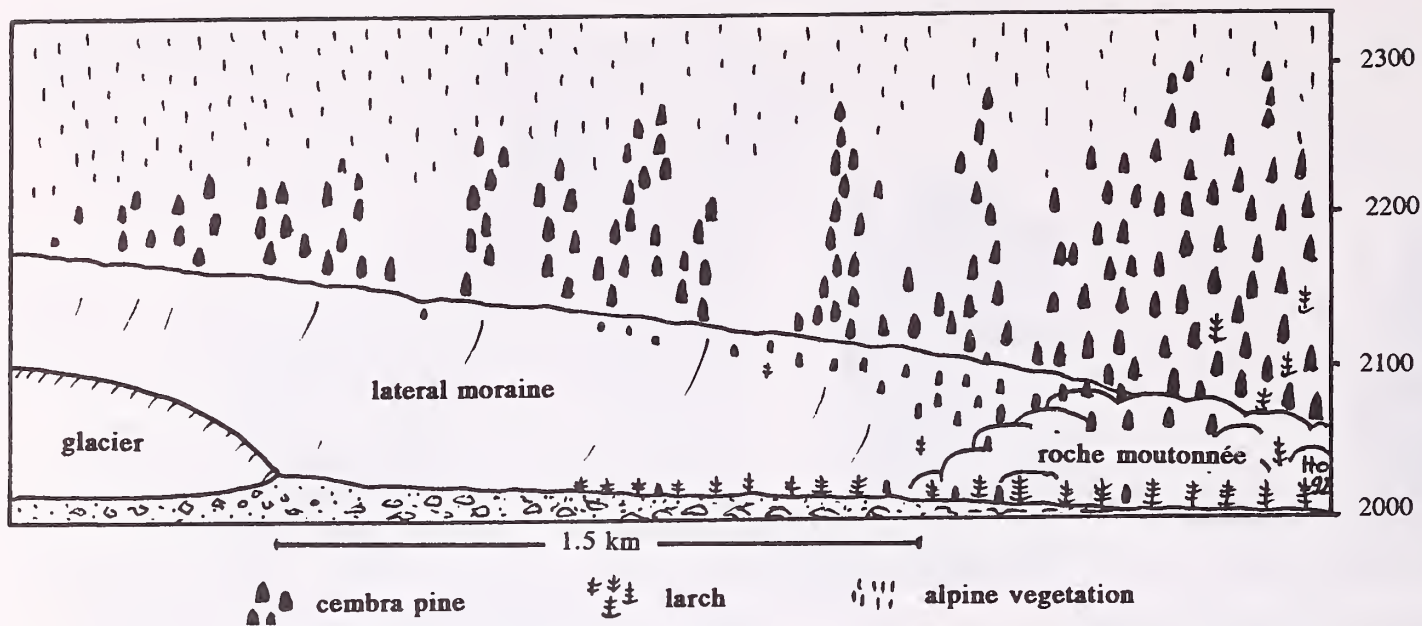


Figure 11—Invasion of the forefield and lateral moraine of the retreating Morteratsch Glacier by cembra pine and larch (schematically).

At places, however, distribution patterns of invading larches and cembra pines very likely depend on soil moisture available, as can be observed in the forefield of Morteratsch Glacier, for example (fig. 11). Obviously, relatively dry sites—such as the well-drained upper part of the lateral moraines or roche moutonnée areas—can be invaded by cembra pine more easily than by larch, because seeds of cembra pine are cached by the nutcracker in small cracks or fine-soil pockets between the boulders where sufficient moisture is available for germination and seedling growth. On the other hand, it depends totally on chance whether wind-mediated larch seeds will get into such a seedbed. At the valley bottom, conditions appear to be more favorable for invasion by larch because of great numbers of open patches of bare mineral soil created by extensive accumulation of fine material between the boulders. At such sites soil moisture is usually available, and there is a better chance for larch seeds to reach a suitable seedbed.

Spruce (*Picea abies*) also occurs within cembra pine-larch forest. Natural stands, however, are confined to the northwest-exposed slope of the main valley between the village of Sils and the small Lake of Staz (fig. 12). This area is characterized by increased humidity due to a cloud belt that usually appears when the Upper Engadine is influenced by moisture-carrying air currents from the southwest (Holtmeier 1965, 1966, 1967). The upper distribution limit of spruce is located at about 2,000 m. Although spruce is missing between Maloja Pass (1,815 m) and Sils, there is some evidence that this species immigrated from the south across Maloja Pass in 6000 to 5500 B.C. (Campbell 1944; Kleiber 1974). The gap can probably be attributed to human influences. On the opposite slope spruce does not occur, except for planted trees (Schlatter 1935). That might be explained by lower humidity and lower soil moisture on that slope exposed to the southeast. Anyway, humans also could have removed shade-giving spruce (Holtmeier 1967). After deglaciation, cembra pine invaded the Upper Engadine earlier than spruce (Kleiber

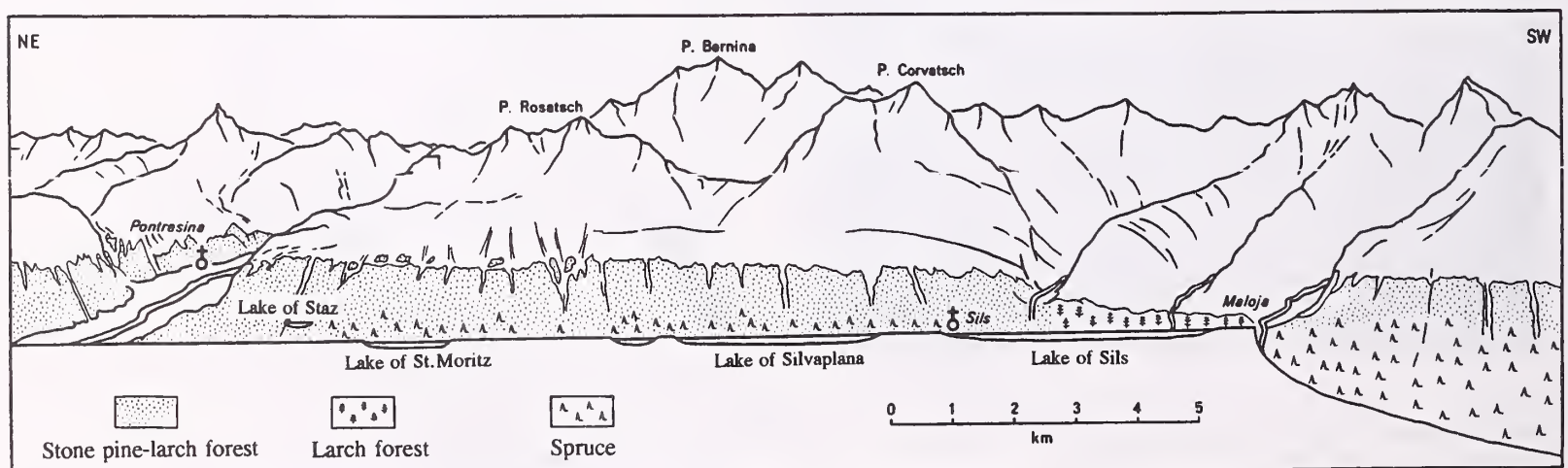


Figure 12—Distribution of spruce (*Picea abies*) on the northwest-exposed slope of the main valley (from Holtmeier 1967, modified).



Figure 13—Arboreous and dwarfed mountain pine in bog near Maloja Pass.

1974). Otherwise it would have been outcompeted by the latter species—at least at lower elevations (Heitz 1975; Mattes 1978).

KRUMMHOLZ SPECIES

Dwarf pine (*Pinus mugo*) and green alder (*Alnus viridis*) form dense and locally extended krummholz stands. The krummholz growth of both these species is genetically predetermined and not climatically induced. That makes them different from climatically trimmed, flagged, and matlike “krummholz” that forms the forest-alpine tundra ecotone in the Rocky Mountains, for example (Holtmeier 1973, 1974, 1981).

Moreover, there is no contiguous *Pinus mugo* krummholz belt above the high-stemmed forest as is peculiar to the northern Alps. In the Upper Engadine, both *Pinus mugo* and *Alnus viridis* occur mainly on slopes endangered by avalanches. Their elasticity enables them to resist avalanches and snow slides better than upright-growing tree species, which normally will be eliminated at such sites. Some slopes, where the original forest had been destroyed by avalanches and fire, were completely

afforested with mountain pine. Mountain pine is also common in bogs where it grows on slightly convex topography (mostly rocky outcrops). At such sites the arboreous growth form also occurs, as is the case on Maloja Pass or in the Lake Staz area, for example (fig. 13).

In general, *Pinus mugo* prevails on limestone and dolomite, while *Alnus viridis* is common mainly on silicate material. In view of this distribution, both species are said to be vicarious plants. In the Upper Engadine, however, the availability of soil moisture seems to be the factor controlling the distribution pattern. There, *Pinus mugo* is more common on southern exposures, whereas *Alnus viridis* is mainly spread on north-facing slopes providing sufficient soil moisture and fresh soils rich in nutrients. On sunny slopes, however, *Alnus viridis* is confined to moist microsites, as alongside rivulets, for example. On northern exposures *Pinus mugo* successfully competes with *Alnus viridis* at sites relatively dry and poor in nutrients (fig. 14).

Birch (*Betula pubescens*) is another species that is usually confined to avalanche tracks and bogs. Birch is able to recover from breakage by thriving basal shoots. Therefore, multistemmed growth is quite common to this species (fig. 15).

At present, the Upper Engadine has a higher forest cover compared to 150 years ago and earlier. Since then many afforestations were carried out to close the gaps caused by historical human impact. Also “exotic” species were used—such as *Picea pungens*, *Picea engelmannii*, *Pinus sibirica*, and others (Schlatter 1935). It has become evident, however, that in this area the native *Pinus cembra* and *Larix decidua* are the most successful species.

CONCLUDING REMARKS

The Upper Engadine belongs to the most important natural ranges of cembra pine-larch forests in the Alps. However, present distribution, composition, and structures of these forests can only be explained by permanent utilization that began in prehistoric time. That makes these forests much different from almost untouched high-altitude forests in remote areas of the Rocky Mountains, for example.

Since tourism has become the main economic base, while agriculture and pastoral land use declined, utilization of the forest also changed. In our day it is not timber production but establishment and maintenance of a vigorous shelter forest (protection from avalanches, soil erosion, torrential washes, etc.) that is the main objective of forest management. Locally, grazing of the high-altitude forest by cattle and game may run counter to the objective and should be reduced as much as possible.

However, the forest also is of great importance for tourism. Thus, larch, which has a high esthetic value because of its bright autumn colors, is favored by special management practices interrupting natural succession. On the other hand, lower elevation forest is still used for production of merchantable timber. Swiss stone pine is used in particular for paneling, carvings, and making furniture of typical local design.

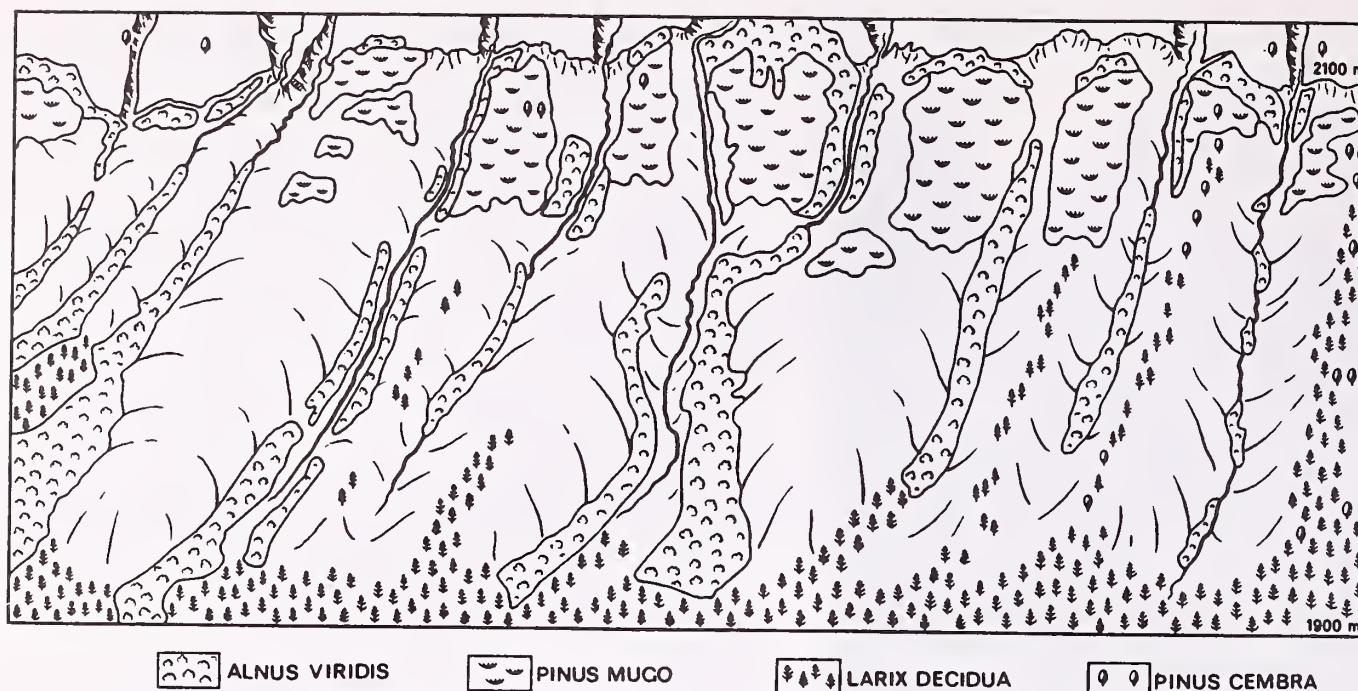


Figure 14—Distribution of *Pinus mugo* and *Alnus viridis* on the northeast-exposed slope of the Bernina Valley. *Pinus mugo* is confined to relatively dry convex topography, while *Alnus viridis* grows on the moist sites (from Holtmeier 1967).

REFERENCES

- Auer, Christian. 1947. Untersuchungen über die natürliche Verjüngung der Lärche im Arven-Lärchenwald des Oberengadins. Mitteilungen der Schweizerischen Anstalt für das forstliche Versuchswesen. 25: 3-140.
- Campell, Eduard. 1944. Der Wald des Oberengadins im Wandel der Zeiten. Festschrift 124. Jahresversammlung der Schweizerischen Naturforschenden Gesellschaft: 93-102.
- Conrad, H. 1940. Beitrag zur Frage der urgeschichtlichen Besiedlung des Engadins. Jahresbericht Historisch-Antiquarische Gesellschaft Graubündens. 70. Jahresbericht: 1-40.

- Ellenberg, Heinz. 1978. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. 2d ed. Stuttgart: Verlag Eugen Ulmer. 981 p.
- Heitz, Christian. 1975. Vegetationsentwicklung und Waldgrenzschwankungen des Spätglazials und Postglazials im Oberhalbstein (Graubünden/Schweiz). Bündnerwald. 28(2): 45-52.
- Holtmeier, Friedrich-Karl. 1965. Die Waldgrenze im Oberengadin in ihrer physiognomischen und ökologischen Differenzierung. University of Bonn, FRG. 163 p. Dissertation.
- Holtmeier, Friedrich-Karl. 1966a. Die Malojaschlange und die Verbreitung der Fichte. Beobachtungen zur Klimaökologie des Oberengadins. Wetter und Leben. 18: 105-108.
- Holtmeier, Friedrich-Karl. 1966b. Die ökologische Funktion des Tannenhähers im Zirben-Lärchenwald und an der Waldgrenze im Oberengadin. Journal für Ornithologie. 4: 253-260.
- Holtmeier, Friedrich-Karl. 1967. Die Verbreitung der Holzarten im Oberengadin unter dem Einfluß des Menschen und des Lokalklimas. Erdkunde. 21: 249-258.
- Holtmeier, Friedrich-Karl. 1973. Geocological aspects of timberlines in Northern and Central Europe. Arctic and Alpine Research. 5(3): 45-54.
- Holtmeier, Friedrich-Karl. 1974. Geökologische Beobachtungen und Studien an der subarktischen und alpinen Waldgrenze in vergleichender Sicht (nördliches Fennoskandien/Zentralalpen). Erdwissenschaftliche Forschung. 8. 130 p.
- Holtmeier, Friedrich-Karl. 1981. What does the term "Krummholz" really mean? Observations with special reference to the Alps and the Colorado Front Range. Mountain Research and Development. 1(3/4): 253-260.
- Holtmeier, Friedrich-Karl. 1990. Disturbance and management in larch-cembra pine forests in Europe. In:



Figure 15—Birch (*Betula pubescens*) growing in an avalanche track.

- Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 25-36.
- Holtmeier, Friedrich-Karl. 1993. European larch in Middle Europe. In: Proceedings—symposium on ecology and management of larch forests: a look ahead. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. [In preparation].
- Kleiber, Helga. 1974. Pollenanalytische Untersuchungen zum Eistrückgang und zur Vegetationsgeschichte im Oberengadin I. *Botanisches Jahrbuch für Systematik*. 94(1): 1-53.
- Mattes, Hermann. 1978. Der Tannenhäher im Engadin—Studien zu seiner ökologischen Funktion im Arvenwald. *Münstersche Geographische Arbeiten*. 2. 87 p.
- Mattes, Hermann. 1982. Die Lebensgemeinschaft von Tannenhäher und Arve. Eidgenössische Anstalt für das forstliche Versuchswesen. *Berichte*. 24. 74 p.
- Oberdorfer, Erich. 1970. Pflanzensoziologische Exkursionsflora für Süddeutschland. 3d ed. Stuttgart: Verlag Eugen Ulmer. 987 p.
- Schlatter, A. J. 1935. Die Aufforstungen und Verbauungen des Oberengadins in den Jahren 1875-1934. *Schweizerische Zeitschrift für Forstwesen*. 86: 309-328.

Evolution and Taxonomy



International Workshop
St. Moritz 1992

GENETIC DIFFERENTIATION AND PHYLOGENY OF STONE PINE SPECIES BASED ON ISOZYME LOCI

Konstantin V. Krutovskii
Dmitri V. Politov
Yuri P. Altukhov

Abstract—F-statistics analysis based on isozyme loci data has revealed comparatively low levels of intraspecific genetic differentiation among natural populations of Eurasian stone pine species: Siberian stone pine (*Pinus sibirica* Du Tour), Korean stone pine (*Pinus koraiensis* Siebold et Zucc.), and Japanese (dwarf Siberian or mountain) stone pine (*Pinus pumila* [Pall.] Regel). Only about 2 to 4 percent of the total isozyme gene diversity was due to interpopulation variation ($F_{ST} = 0.021-0.040$), and the overwhelming part of the total variation, over 96 percent, belonged to intrapopulation variation. These data are discussed in relation to distinguishing features of conifer biology, in general, and to a specific mode of stone pine seed distribution by nutcrackers, in particular. Cluster analysis of more-studied Siberian stone pine populations has shown that genetic distances based on isozyme allele frequencies reflect geographical distribution of these populations in spite of the generally low values of genetic distances ($D = 0.001-0.031$, on the average of 0.006).

The authors have studied phylogenetic relationships between all stone pine species (subsection *Cembrae*), including one European stone pine population—Swiss stone pine (*Pinus cembra* L.) and one population of the only representative of stone pine species in North America—whitebark pine (*Pinus albicaulis* Engelm.), using genetic distances based on 16 isozyme loci, whose genetic control has been resolved for all stone pine species. The results have confirmed stone pine (*Cembrae*) species to be a compact group of very closely related and genetically similar species, having monophyletic origin, supposedly from ancient Siberian stone pine. The smallest distance ($D = 0.065$) has been found between *Pinus cembra* and *Pinus sibirica* that corresponded, mostly, to their subspecies taxonomic status. Other interspecific distances were in good agreement with the species status ($D = 0.121-0.268$).

As to the controversy on the taxonomy of whitebark pine, this species undoubtedly belongs to subsection *Cembrae* ($D = 0.121-0.256$). The results of phylogenetic study have been confirmed by the recently obtained data of cpDNA restriction fragment analyses.

Five stone pine species are traditionally united in subsection *Cembrae* of section *Strobus*, subgenus *Strobus*, genus *Pinus* (Critchfield and Little 1966; Shaw 1914). European or Swiss stone pine (*Pinus cembra*) is distributed in the Alps and Carpathians and has the smallest area among stone pine species. An east Asian stone pine species, Korean pine (*P. koraiensis*), is widely distributed in eastern Russia (Russian "Far East"), Manchuria, and Japan, but mostly in Korea. Two other stone pine species are: Japanese stone pine (*P. pumila*), widely distributed in northeastern Siberia extending to eastern Asia, as far as central Japan; and Siberian stone pine (*P. sibirica*), widely distributed, mostly in Siberia extending to northern Mongolia and to the eastern border of Europe. Whitebark pine (*P. albicaulis*) is widely distributed in western North America, extending from British Columbia to the southern Sierra Nevada, and represents the only stone pine species growing outside Eurasia.

All these species are of great interest for different kinds of investigations, but some main aspects make these species very attractive from evolutionary and population genetics points of view and explain the necessity of their genetic study.

First, they occupy a vast territory in Eurasia and North America and most of them belong to the main forest-forming species. Thus, they have great ecological and economic significance, especially in Eurasia. They are subjected to intensive harvesting and, consequently, need special breeding and gene conservation programs based on genetic data.

Second, stone pine species consist of different kinds of populations. For example, Swiss stone pine includes mostly small, isolated populations and occupies a relatively small territory. On the other hand, Siberian stone pine includes huge, continuous populations occupying a very large territory in Siberia. Some of the stone pine species are completely isolated from others: Swiss stone pine, growing in Europe, and whitebark pine, growing in North America, stand apart from Asian stone pine species. At the same time, Siberian, Korean, and Japanese stone pines have sympatric zones. Thus, from evolutionary and population genetics points of view and for gene conservation programs it would be interesting and important to study genetic differentiation, gene dispersal patterns, and mating system and population genetic structure of these species and compare them with each other.

Third, in spite of the fact that stone pines have a wide geographical distribution and some morphological and ecological differences, they are grouped into a separate subsection *Cembrae*, because they have some diagnostic

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Konstantin V. Krutovskii is Senior Research Scientist, Laboratory of Population Genetics, N.I. Vavilov Institute of General Genetics, Russian Academy of Sciences, GSP-1 Moscow 117809 B-333, Russia (current address until 1995: Department of Forest Genetics and Tree Improvement, Georg-August-University, Büsgenweg 2, Göttingen, 37077, Germany); Dmitri V. Politov is Research Scientist, same laboratory; Yuri P. Altukhov is Professor, Member of Russian Academy of Sciences, Head of the Laboratory of Population Genetics, Director of the Institute of General Genetics.

morphological traits that distinguish them from other *Strobos* species. Most significant of these are wingless large seeds and indehiscent cones that remain closed in maturity. These traits are supposed to be the result of long co-evolution of stone pines and nutcrackers (*Nucifraga* ssp.), who play a crucial role in natural reproduction and distribution of stone pine species (Lanner 1980, 1982, 1990; Tomback 1983; Tomback and Linhart 1990; Tomback and others 1990). Nevertheless, taxonomy of these species is still being discussed. Some specialists consider Swiss stone pine a subspecies of Siberian stone pine (or vice versa) and some think that whitebark pine should be included into subsection *Strobi* because of its morphological and ecological resemblance to some *Strobi* species (Critchfield 1986; Millar and Kinloch 1991). Taking all this into account, the use of genetic markers for study of phylogenetic relationships between stone pine species would be very appropriate and fruitful.

Thus, the main tasks of our research were estimation of genetic differentiation and subdivision of stone pine populations and study of phylogenetic relationships between stone pine species using isozyme loci as genetic markers.

The advantages and disadvantages of using isozymes in plant systematics and phylogeny have been fairly thoroughly discussed in scientific literature (see for example, Crawford 1983; Gottlieb 1977; Strauss and others 1992). We would only like to note here such taxonomically most important advantages as, first, the possibility of using the same trait (isozyme electrophoretic pattern encoded by homologous loci) to classify taxons of almost any phylogenetic level, both related and unrelated, and second, the possibility of quantitative estimation of divergence degree. One of the problems of traditional systematics is associated with the objective choice of diagnostic traits, but initial selection of such traits usually leads to their preliminary "weighting" (evaluation) and inevitably produces subjectivity. It is, therefore, extremely important to use, above all, such traits in taxonomic studies as can be taken for analysis without "weighting," more or less arbitrarily, and about whose variability nothing has been known a priori. Molecular genetic markers (isozyme loci and DNA markers) are one of the best, from these points of view.

The study presented here is the first one devoted to study of phylogeny of the whole subsection *Cembrae* using isozyme markers and is only a part of long-term studies on population genetics of stone pine species carried out in the Laboratory of Population Genetics of N. I. Vavilov Institute of General Genetics (Russian Academy of Sciences, Moscow, Russia) on the basis of isozyme analysis. More details on inheritance and linkage of isozyme loci, mating system, population genetic structure, and other aspects of stone pine population genetics can be found in our previously published papers (Krutovskii and Politov 1992; Krutovskii and others 1987, 1988, 1989, 1990; Politov 1989; Politov and Krutovskii 1990; Politov and others 1989, 1992) and in the accompanying paper included in these proceedings by Politov and Krutovskii.

MATERIAL AND SAMPLING SITES

Seventeen single-tree and two bulk seed samples from natural populations have been used for isozyme analysis in our study. Eleven localities of Siberian stone pine, three

localities each of Korean and Japanese stone pines, and one locality each of Swiss stone and whitebark pines have been studied on 16-20 isozyme loci (table 1). More details about seed samples and characteristics of the sampled natural populations can be found in our other publications (Krutovskii and Politov 1992; Krutovskii and others 1988, 1989, 1990; Politov 1989; Politov and Krutovskii 1993; Politov and others 1992).

ELECTROPHORETIC ANALYSIS

Isozymes of seeds have been studied by electrophoresis in starch gel. Method of electrophoretic analysis, specimen preparation, the buffer systems used, genetic interpretation of zymograms, designations of allozymes, alleles, and loci, and inheritance of enzyme systems have been described elsewhere (Krutovskii and others 1987; Politov 1989). Genotypes of trees have been determined by analyzing segregation of allozyme alleles among their endosperms, which are haploid in conifers and genetically identical to maternal tree gametes. Together with adult tree allele frequencies, pollen allele frequencies inferred from effective pollen gene pool (paternal alleles of the analyzed seed embryos) have been used for estimation of genetic distances. These frequencies of successful pollen give probably more representative estimation of the studied populations' gene pools due to predominantly outcrossing pollination among stone pine species (Politov and Krutovskii 1990, 1993).

In total, 536 trees from 17 localities (11-75 trees each) and two bulk seed samples of five stone pine species have been analyzed on 16-20 isozyme loci. More than 3,500 (7-20 per tree) embryos have been analyzed on a smaller amount of isozyme loci because of poor resolution of some enzyme systems in embryo tissue. A relatively small number of trees have been analyzed in some populations and species, but according to some theoretical (Nei 1987a,b) and experimental investigations (Shurkhal and others 1992), the number of loci used in interspecific phylogenetic analysis is more important than the sample size. We have studied phylogenetic relationships between all stone pine species using genetic distances based on 16 isozyme loci, Adh-1, Dia-2, Fe-2, Gdh, Got-1, Got-2, Got-3, Idh, Mdh-1, Mdh-2, Mdh-3, Mdh-4, Pgi-2, Pgm-1, Pgm-2, and Skdh-1, whose allelic variation has been unequivocally determined for all stone pine species. Such a number of loci is used commonly and gives quite reasonable phylogenetic trees (Nei 1987a,b).

DATA ANALYSIS

Determination of parameters of intra- and interpopulational genetic diversity, estimation of genetic differentiation and genetic distances, and clustering and construction of dendrograms for stone pine populations have been carried out by using IBM PC version 1.7 of the computer program BIOSYS-1 (Swofford and Selander 1981) and IBM PC-program RESTSITE, version 1.1 (Nei and Miller 1990).

Using our data, we have estimated different kinds of genetic distances and tried different methods of clustering. Methods for calculating genetic distances and methods of clustering differ in their assumptions concerning homogeneity of evolutionary rates or proportionality to the time of divergence. Consequently, topology of derived phylogenetic

Table 1—Name, abbreviated designation, sample size, and geographic location of sampling sites

Locality	Designation	Number of trees	Region
Siberian Stone Pine			
Filin Klyuch	F	53	Western Sayan Mountains (Ermakovskii District, Krasnoyarsk Territory, eastern Siberia)
Mutnaya Rechka	M	75	
Malyi Kebezh	MK	15	
Sobach'ya Rechka	SR	12	
Listvyanka	L	41	
Yailyu	YA	43	Altai Mountains (Gorno-Altayskaya Autonomous Region, eastern Siberia)
Smokotino	S	43	Tomskaya Region (western Siberia)
Zorkal'tsevo-1	Z-1	34	
Zorkal'tsevo-3	Z-3	34	
Turukhansk	TU	100	North of Krasnoyarsk Territory, (Turukhanskii District, North of eastern Siberia)
Nyalino	NYA	188	Khanty-Mansi Autonomous District (Tyumenskaya Region, North of western Siberia)
Swiss Stone Pine			
Ust'-Chornaya	UCH	15	Eastern Carpathians (western Ukraine)
Japanese Stone Pine			
Grustnyi	GR	54	North of Kamchatka Peninsula
Utyveem	UT	55	
Kamenskoye	K	55	
Korean Stone Pine			
Malokhekhtsirskoye	MKH	30	Khabarovsk Territory
Khor	KHO	16	(Russian "Far East")
Sikhote-Alin ¹	SA	11	Primorskii Territory (Russian "Far East")
Whitebark Pine			
Livingstone Falls	LF	52	Rocky Mountains Forest Reserve, Bow-Crow Forest (southwestern Alberta, Canada)

¹Number of analyzed seeds from mixed sample obtained from large number (>100) of trees.

trees based on different distances and methods of clustering can vary significantly for the same data.

Among methods of clustering that assume homogeneity of evolutionary rates, an unweighted pair group method using arithmetic averages, UPGMA, is the most widely used one (Sneath and Sokal 1973). Among methods that do not assume homogeneity of evolutionary rates, the distance Wagner procedure (Farris 1972) and neighbor-joining method, NJM (Saitou and Nei 1987) are the most widely used ones.

The most common genetic distances used in isozyme studies of trees are Nei's (Nei 1972, 1978), Rogers' (1972), and Cavalli-Sforza and Edwards' (1967) distances. However, Nei's distance, D , along with advantages has some disadvantages, the main one being that it is not metric because it does not obey the triangle inequality and, consequently, cannot be used in the distance Wagner procedure or NJM. Thus, we have used D (Nei 1972) only in UPGMA dendrograms.

Taking into account: (1) that homogeneity of evolutionary (or allozyme allele substitution) rates can usually be safely assumed in comparing conspecific populations of widespread, continuous tree species with high gene flow, like stone pine populations; (2) shortage of space for presentation of all obtained dendrograms; and (3) possibility for wider comparison with published data, we will present only UPGMA dendrograms based on Nei's distance, D , for analysis of intraspecies stone pine population relationships. However, to avoid problems connected with possible nonhomogeneity of evolutionary rates of different species, we will present NJM dendrograms of stone pine species based on Cavalli-Sforza and Edwards' (1967) chord distances, D_{ch} , in addition to UPGMA dendrograms based on D and D_{ch} .

Nei's genetic distances matrix has also been used for principal coordinate analysis of Siberian stone pine populations using the computer program NTSYS-pc (Rohlf 1988).

INTRASPECIFIC DIFFERENTIATION

Levels of Genetic Differentiation Between Populations—Distribution of intraspecific genetic variation between populations of stone pines has been analyzed for three species studied in several localities using F-statistics (Nei 1977). Levels of genetic differentiation among populations were comparatively low—only about 2-4 percent of the total intraspecific isozyme gene variation was due to interpopulation variation ($F_{ST} = 0.021-0.040$), and the overwhelming part of the total variation, over 96 percent, belonged to intrapopulation variation (table 2). Loci Fe-2, Mdh-3, and Skdh-1 of Siberian stone pine, Adh-1, Adh-2, Gdh, Got-2, Mdh-2, Mdh-3, Mdh-4, and Skdh-2 of Japanese stone pine, and Mdh-4 of Korean stone pine make a most significant contribution in intraspecific differentiation of these species (table 2). The geographic variation of these loci may be adaptive and should be studied in detail in future investigations.

Nei's genetic distances between populations were also small, $D = 0.001-0.031$ and 0.012 , on the average (table 3). These values correspond perfectly to the calculations carried out using references on 22 pine species (Altukhov and others 1989). The genetic distances between closely located (<20 km) populations of seven pine species equaled 0.009 , on the average, and between widely dispersed populations of 15 pine species reviewed— $D = 0.036$, on average.

Low levels of interpopulation differentiation of allozyme loci are usual for conifers. Such typical factors for most conifer populations as outcrossing, wind pollination, seed dispersal by wind (most conifers) or by birds (stone pines, some white pines, and pinyons), wide continuous ranges, high population density, and effective size are considered to reduce the influence of genetic drift and, therefore, decrease

heterogeneity of allele frequencies and interpopulation genetic differentiation (Hamrick 1983; Hamrick and Godt 1989; Hamrick and Loveless 1986; Hamrick and others 1981; Loveless and Hamrick 1984).

We have also summarized data on interpopulation genetic differentiation of 28 conifer species of eight genera estimated using F_{ST} or analogous G_{ST} parameters of differentiation (Politov and others 1992). In spite of a, generally, comparatively low differentiation among populations, we have found a quite pronounced tendency to a significantly smaller differentiation ($F_{ST} = 0.02-0.08$) among widespread species with continuous population ranges than among species with interrupted ranges and small, and often isolated, populations ($F_{ST} = 0.11-0.13$). Moreover, according to our review, samples from the same population (samples from localities within several kilometers radius) revealed, commonly, an even much lower level of differentiation ($F_{ST} = 0.006-0.02$).

The three stone pine species studied belong to the first group of species with mainly continuous population range. Besides, four of the 11 Siberian stone pine samples, F, M, MK, and SR, have been collected within 20 km radius from obviously the same population of Malyi Kebezh River Basin (eastern Siberia, table 1); and the other two samples have been taken from two stands near Zorkal'tsevo village (western Siberia), Z-1 and Z-3, which are separated from each other by less than 3 km. The other localities are rather remote from one another, but all of them represent only the central, continuous part of the species area. There are no significant barriers to gene flow in this area.

The low differentiation observed in our study may also be due to the limited number of samples taken, mostly, from more or less optimal zones of the stone pines area, impeding the diversifying selection action and promoting the balancing one (Altukhov 1990).

Table 2—The estimates of F-statistics for populations of three stone pine species and for all five species

Locus	Siberian stone pine			Korean stone pine			Japanese stone pine			All
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}	F_{ST}
Adh-1	-0.030	-0.006	0.023	0.078	0.120	0.045	0.306	0.321	¹ 0.022	¹ 0.563
Adh-2	(²)	(²)	(²)	(²)	(²)	(²)	-0.068	-0.046	¹ 0.020	—
Dia-1	-0.032	-0.007	.024	(²)	(²)	(²)	(²)	(²)	(²)	—
Dia-2	-0.060	-0.053	.006	(³)	(³)	(³)	-0.038	-0.013	¹ 0.025	¹ 0.028
Fe-2	-0.061	-0.012	¹ 0.046	-0.067	-0.021	.043	-0.105	-0.097	.007	¹ 0.190
Gdh	-0.012	-0.001	.010	-0.098	-0.098	.000	.084	.140	¹ 0.061	¹ 0.637
Got-1	-0.013	-0.001	.012	(³)	(³)	(³)	(³)	(³)	(³)	.002
Got-2	-0.012	-0.001	.010	(³)	(³)	(³)	-0.050	-0.022	¹ 0.027	¹ 0.016
Got-3	(³)	(³)	(³)	.238	.241	.004	.014	.015	.001	¹ 0.596
Lap-2	.015	.025	.009	-0.071	-0.023	.045	-0.048	-0.047	.001	—
Lap-3	.066	.079	.013	(²)	(²)	(²)	-0.064	-0.050	.013	—
Mdh-2	.214	.231	.023	-0.251	-0.225	.020	-0.004	.015	¹ 0.019	¹ 0.240
Mdh-3	-0.049	.000	¹ 0.047	-0.067	-0.021	.043	-0.051	.084	¹ 0.128	¹ 0.118
Mdh-4	-0.068	-0.055	.012	.017	.104	¹ 0.089	-0.021	-0.013	¹ 0.008	¹ 0.362
Pgi-2	.114	.123	.010	(³)	(³)	(³)	-0.111	-0.107	.003	¹ 0.407
Pgm-1	-0.074	.051	.022	-0.193	-0.160	.028	.177	.189	.016	¹ 0.187
Pgm-2	(³)	(³)	(³)	(³)	(³)	(³)	-0.014	-0.013	.002	¹ 0.046
Skdh-1	-0.146	-0.118	¹ 0.025	-0.316	-0.194	.092	-0.053	-0.051	.002	¹ 0.187
Skdh-2	(²)	(²)	(²)	(³)	(³)	(³)	.099	.163	¹ 0.071	—
Mean	-.043	-.018	.025	-.077	-.033	.040	-.002	.020	.021	.396

¹This locus has statistically significant heterogeneity of allele frequencies among populations.

²The genetic base of isozyme variation of this locus is not determined or allelic variation cannot be compared with other species.

³This locus is monomorphic in this species.

Table 3—Genetic distances, D, (Nei 1972) for five stone pine species

Species	N ¹	Siberian stone pine	Swiss stone pine	Japanese stone pine	Korean stone pine
Siberian stone pine	11	0.006 (0.002-0.016)			
Swiss stone pine	1	0.065 (0.055-0.077)			
Japanese stone pine	3	0.202 (0.176-0.253)	0.233 (0.215-0.265)	0.010 (0.003-0.014)	
Korean stone pine	3	0.235 (0.207-0.261)	0.268 (0.264-0.275)	0.105 (0.096-0.119)	0.009 (0.004-0.014)
Whitebark pine	1	0.121 (0.111-0.129)	0.130 —	0.185 (0.166-0.220)	0.256 (0.253-0.261)

¹N = number of localities studied.

And finally, the low differentiation between stone pine populations can be considered the result of a specific mode of seed dispersal by nutcrackers able to carry their seeds over very long distances (up to 20 km, according to some observations). The efficiency of this mode and its influence on the population structure were repeatedly emphasized by researchers studying relationships between nutcrackers and whitebark pine, Swiss stone pine, limber pine (*Pinus flexilis* James), and pinyons (subsection *Cembroides*) (Carsey and Tomback 1992; Fournier and others 1987; Lanner 1980, 1990; Schuster and Mitton 1991; Tomback and others 1990, 1992).

Cluster and Principal Coordinates Analysis—

Despite the low values of genetic distances, UPGMA clustering of stone pine samples based on these distances reflects, in general, their geographical origin. More detailed analyses have been performed on Siberian stone pine, which has been studied more than other stone pines. We can tentatively divide all 11 Siberian stone pine localities into three regions, according to their ecology and geographic location. The first of them can be called “Southern Siberia Mountains” and includes one population from the Altai Mountains (Ya) and five localities in the western Sayan (FK, M, MK, SR, and L); the second can be called “Western Siberia Plain” and includes populations from Tomsk region (S, Z-1, and Z-3); the third, “Northern Siberia,” includes populations from Khanty-Mansi Autonomous District (NYa) and from the north of Krasnoyarsk Territory (TU). The dendrogram obtained corresponds exactly to this classification (fig. 1). These three regions form three different genetic groups (clusters) of populations.

Korean pine samples also form clusters in accordance with their population localization (two geographically more closely spaced stands, MKh and Kho, have turned out to be genetically more similar). The same is true of Japanese stone pine populations (fig. 1). Principal coordinates analyses based on the matrix of Nei's genetic distances between Siberian stone pine populations also have been performed. This multidimensional analysis has produced almost the same result as the cluster analysis. Genetic relationships between Siberian stone pine populations, graphically presented in two-dimensional space of the first two principal coordinates, have perfectly reflected the real geographical

distribution of these populations (fig. 2). Principal coordinates and cluster analyses complement each other and have produced almost the same result in our case, but the first, probably, gives more information about population genetic relationships due to better data presentation. Multivariate analysis techniques are supposed to provide, basically, better possibility for revealing genetic differentiation in conifers, as compared to univariate methods (Krutovskii and Politov 1992; Yeh and others 1985).

Statistically significant positive correlation between geographical and genetic distances has been found for Siberian stone pine populations ($r = 0.844$, $P < 0.001$). Such correlation was, however, absent for samples from closely spaced localities of the Malyy Kebezh River Basin. The limited number of samples studied has not allowed such analysis for other stone pine species, but analogous results have

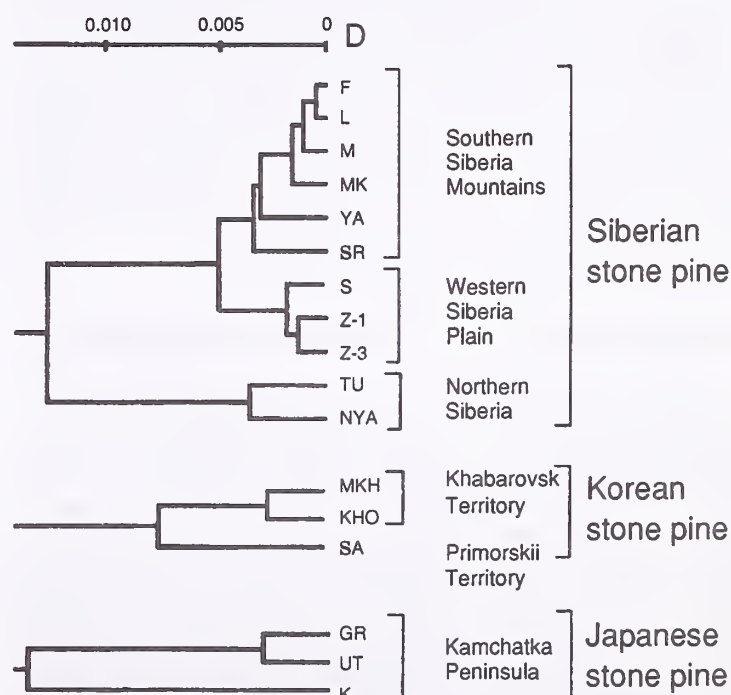


Figure 1—UPGMA phenograms of stone pine populations based on Nei's genetic distances, D, (Nei 1972). (See full names and origins of populations in table 1.)

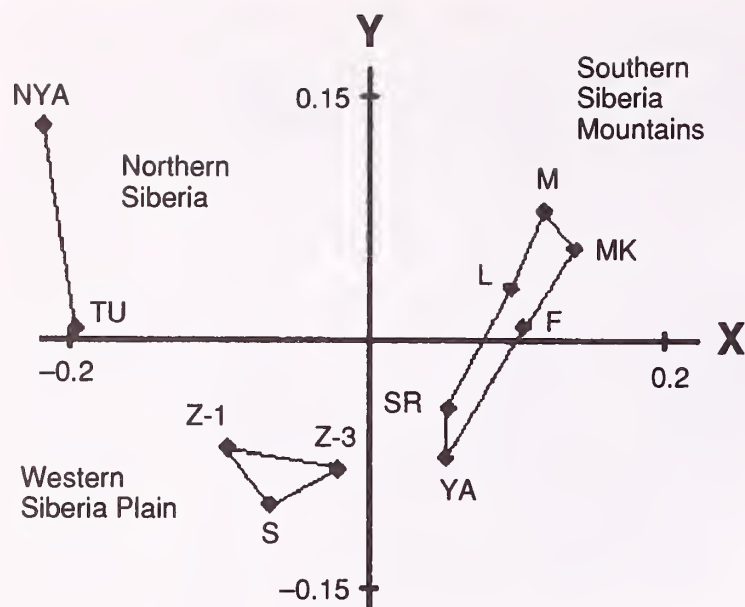


Figure 2—Projections of Siberian stone pine populations in two-dimensional space of the first two principal coordinates, X and Y, according to Nei's genetic distances, D , (Nei 1972). (See full names and origins of populations in table 1.)

also been obtained for some other pine species (Furnier and Adams 1986; Steinhoff and others 1983; Wheeler and Guries 1982), including, probably, that isolation by distance (Nei 1975), introgressive hybridization (Millar 1983), or gradiently changing selection (Bergmann 1978) could play a significant role in genetic differentiation of some pine species.

We have also analyzed correlation between geographical and Nei's distances calculated for Siberian stone pine populations using data on individual loci (allele frequencies of eight loci in the effective pollen pool have been used). For loci *Adh-1*, *Dia-2*, *Fe-2*, *Pgm-1*, and *Skdh-1* correlation was significant. The other loci (*Lap-3*, *Mdh-2*, and *Pgi-2*) displayed lack of correlation. This may suggest a selective role of certain loci. Patterns of spatial differentiations seem to be determined by complex interaction of gene flow and selection. Distribution of genetic variability may be also affected by "evolutionary footprints," such as, for example, Siberian population descent from different refugia.

INTERSPECIFIC DIFFERENTIATION

Genetic Distances Between Stone Pine Species—

We have estimated both genetic distances, D_{ch} and D , between all stone pine species based on 16 isozyme loci data, but only D values are presented in table 3, because of space limits. The smallest genetic distances have been found between Siberian and Swiss stone pines ($D = 0.052-0.077$). They are just a little larger than those between subspecies of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), $D = 0.008-0.019$, approximately 0.012 on the average (Wheeler and others 1983), similar to the distances between subspecies of brutian pine (*Pinus brutia* Ten.), $D = 0.03-0.09$ (Conkle and others 1988), and a little smaller than distances between two very closely related species, jack pine (*Pinus banksiana* Lamb.) and lodgepole pine, which have a wide zone of introgressive hybridization, $D = 0.097$, according to

the study by Dancik and Yeh (1983), or $D = 0.108$, according to Wheeler and Guries (1987). Nei's distances estimated between other pairs of stone pine species ($D = 0.121-0.268$, table 3) are close to the values reported for pine species of subsections *Contortae*: 0.078-0.158 (Wheeler and others 1983) and *Oocarpae*: 0.11-0.27 (Millar and others 1988). Approximately the same value, $D = 0.27-0.43$, has been reported for *Pinus brutia*-*Pinus halepensis* comparison (Conkle and others 1988). We have estimated the average genetic distance between species from the same subsections using a few references (Conkle and others 1988; Millar and others 1988; and some others). It equaled 0.185, on the average, for 14 pine species and surprisingly corresponded to the average distance estimated for all stone pine species in our study— $D = 0.180$, and for four Eurasian stone pine species studied by Shurkhal and others (1991a,b)— $D = 0.138$ (for comparison, $D = 0.185$, on the average, for four Eurasian stone pines used in our study). The small discrepancy between the latter two estimates is not surprising, taking into account the sampling strategy used by Shurkhal and others (1991a,b; 1992). They have analyzed only a few trees of each species (mostly, from Botanical Garden collections), which should inevitably bias genetic distance estimates to smaller values, due to a higher probability of random fixation of most common, frequent alleles in small samples of trees from different species.

Levels of interspecific genetic differentiation obtained between stone pines strongly confirm their taxonomical status as closely related species of the same subsection. Nei's genetic distances obtained for species belonging to different subsections or sections are usually higher than 0.3 and vary between 0.3 and 0.8 (Shurkhal and others 1991a,b; 1992). According to phylogenetic analysis carried out by Shurkhal and others (1991a,b; 1992) using isozyme loci, four stone pine species of subsection *Cembrae* (white-bark pine has not been analyzed) and three white pine species of subsection *Strobi*, Balkan or Macedonian pine (*Pinus peuce* Griseb.), blue or Himalayan pine (*Pinus griffithii* McClelland), and eastern white or Weymouth pine (*Pinus strobus* L.), form separate clusters. The Nei's genetic distance between these two very closely related subsections equals 0.278, on the average (calculated by us, using the data in table 5 from Shurkhal and others 1991b). This is almost two times larger than that between Eurasian stone pines ($D = 0.138$).

The lack of species-specific diagnostic loci among stone pines also confirms the correctness of uniting them in the same separate subsection *Cembrae*. Only Siberian and Korean stone pines, on locus *Gdh*, and Swiss and Korean stone pines, on locus *Mdh-4*, do not have common alleles. Besides, Korean stone pines have a unique electrophoretic pattern of LAP enzyme indicating the existence (or expression) of an additional *Lap-4* locus.

Loci *Adh-1*, *Gdh*, *Got-3*, *Mdh-4*, and *Pgi-2* make a most significant contribution to interspecific differentiation of stone pines, but totally only 39 percent of the whole subsection *Cembrae* genetic variation belongs to interspecific differences (table 2).

Thus, our data give a strong genetic evidence of common, apparently monophyletic stone pines origin and comparatively recent time of their divergence. Subsection *Cembrae* seems to be a valid taxon.

Phylogenetic Relationships Inferred From Genetic Distances—Many publications have been devoted to studies of taxonomic and phylogenetic relationships between stone pines using morphological, physiological, ecological, and other traits. Our study was the first one to use genetic markers, isozyme loci, for analysis of phylogenetic relationships between all five stone pine species. These species are traditionally united in subsection *Cembrae*, according to some characteristic features (Critchfield and Little 1966; Farjon 1984; Little and Critchfield 1969; Shaw 1914). The overwhelming majority of researchers consider the main specific features of this subsection, indehiscent cones and wingless seeds, to be inherited from a common ancestor. These traits seem to be a relatively recent acquisition. Their appearance is considered to be a result of coevolution of stone pines and nutcrackers of genus *Nucifraga* foraging their seeds and playing the main role in their maintenance and dispersal (Lanner 1980, 1982, 1990; Tomback 1983; Tomback and Linhart 1990; Tomback and others 1990).

Thus, the subsection *Cembrae* is regarded as a natural monophyletic taxon. Nevertheless, there also exists a different point of view (Critchfield 1986), according to which traits shared by all stone pines are insufficiently confirmed as homologous. Data on artificial hybridization appear to be rather contradictory (Critchfield 1986). The subsection is believed to have polyphyletic origin and, therefore, is not a valid taxon (see for discussion, Lanner 1990). Millar and Kinloch (1991) also have pointed out a number of unsolved problems in taxonomy and phylogeny of subsection *Cembrae*.

Molecular and biochemical genetic markers have proven to be a useful tool for study of biosystematic and phylogenetic relationships in conifers (Strauss and others 1992). We believe that application of biochemical genetic markers like isozymes can help shed light on the evolution of stone pine species. The dendrograms produced by NJM and UPGMA clustering using D_{ch} and D matrix (table 3) based on 16 isozyme loci have apparently revealed real phylogenetic relationships between five stone pine species (fig. 3).

According to this dendrogram, Siberian and Swiss stone pines appear to be a most closely related pair of species ($D = 0.065$). This was not unexpected, because of the well-known surprisingly high morphological similarity (Bobrov 1978) and successful artificial hybridization (Critchfield 1986) between them. Practically all traditional botanical classifications note the absence of diagnostic morphological traits, which means that interspecific differences are more quantitative than qualitative. According to paleobotanical (mainly palynological) data, Bobrov (1978) considered these two species as two now separately located marginal parts of a former single ancestral species spread on a vast range area, from the western Alps to the northeastern Yakutia (eastern Siberia), whose pollen has been found in Paleocene, Pleistocene, and later deposits.

As Bobrov (1978) indicates, "Siberian stone pine must be regarded as the initial, more ancient species, formerly more widely distributed, whereas the West European stone pine, *Pinus cembra*, is evolutionarily still very young and has become geographically isolated in the recent past, being, therefore, hardly distinguishable from its Siberian ancestors."

Breakup of this ancient range, its division into two parts, and decrease of its western part occurred, most likely, as

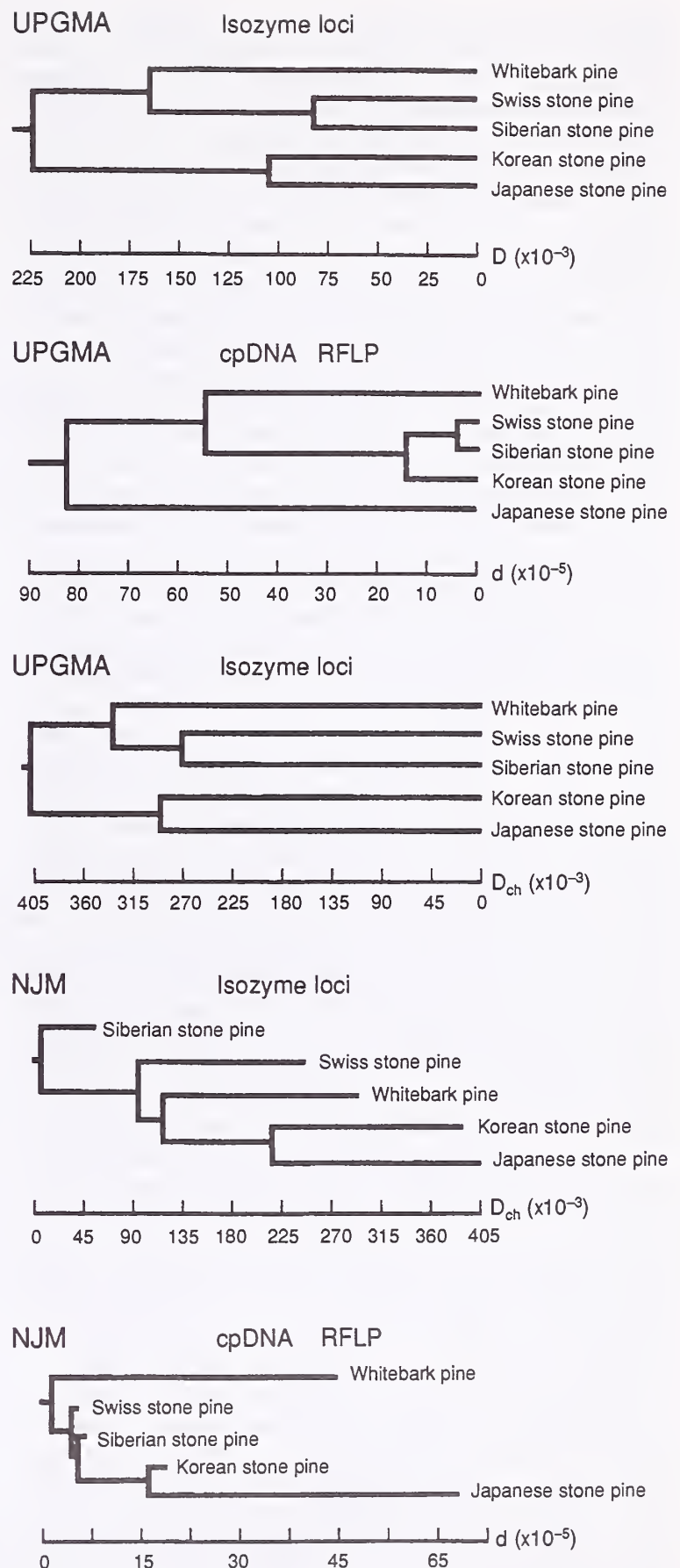


Figure 3—UPGMA and NJM dendrograms of five stone pine species (subsection *Cembrae*) based on Cavalli-Sforza and Edwards' (1967) and Nei's (Nei 1972) genetic distances, D_{ch} and D , calculated from isozyme data, and on d (Nei 1987b; Nei and Miller 1990), calculated from chloroplast (cp) DNA restriction fragment length polymorphism (RFLP) data (Krutovskii and Wagner 1993).

late as in the Holocene and was associated with its substitution in the central part of the area by other species due to the global warming. The time of divergence (10,000 to 25,000 years), estimated from the genetic distance between Siberian and Swiss stone pines corresponds, approximately, to these events (for more details see Krutovskii and others 1990). Thus, the low level of divergence between Siberian and Swiss stone pines can be explained by the short time of isolation.

Nevertheless, a considerable amount of genetic difference has accumulated during this time—genetic distances between Siberian and Swiss stone pines are approximately 10 times larger than those between populations of the same species (table 3) and are comparable with distances reported by Conkle and others (1988) for subspecies and very closely related pine species. Our data have also been recently confirmed by Goncharenko and others (1992) and Shurkhal and others (1991a,b; 1992). Their estimates of Nei's genetic distance between Siberian and Swiss stone pines equaled 0.030 and 0.042, correspondingly. Thus, Swiss stone pine seems to be a highly diverged geographical race or subspecies of Siberian stone pine, or a species *in statu nascendi*.

Unexpectedly relatively small differentiation found between Japanese and Korean stone pines ($D = 0.105$) makes us search for a new approach to understanding their origin. These species, in fact, have little in common in morphology of both vegetative and generative organs, but according to the study of parenchymal tissue of needle cell walls, stone pine species and some closely related species can be divided into two types: Siberian and Swiss stone pine form the first type, while Japanese and Korean stone pines belong to the second type, but to different subtypes (Litvintseva 1974). Perhaps, the evolutionary pathways of these species have truly separated from a common ancestor relatively recently. Another explanation of their genetic similarity is gene exchange through introgressive hybridization, which could have occurred (or seldom occurs), taking into account the present sympatry of these species and, as a rule, poorly developed mechanisms of reproduction isolation between closely related pine species. More detailed discussion can be found in Krutovskii and others (1990), but recently obtained data also confirm the division of Eurasian stone pines by isozyme loci analysis into two groups: Siberian and Swiss stone pines ($D = 0.030-0.042$), on one hand, and Korean and Japanese ($D = 0.089-0.143$), on the other hand (Goncharenko and others 1992; Shurkhal and others 1991a,b; 1992).

A most interesting problem, from our point of view, is explanation of the whitebark pine's closer affinity to Siberian and Swiss stone pines ($D = 0.121-0.130$) than to Japanese stone pine ($D = 0.185$), although quite opposite relationships could be suspected considering these species' present area. Among stone pines Siberian and Swiss stone pines are, probably, genetically most similar to the original ancient stone pine, due to large refugia in the Alps and Siberian (Altai and Sayan) Mountains, which could help them save a great deal of ancient genetic variation; and whitebark pine also could keep more genetic similarity with the ancient species than Korean and Japanese stone pines. Another explanation could be that stabilizing selection supports genetic similarity between whitebark pine and Siberian and Swiss stone pines, because whitebark pine ecologically

has, probably, more in common with them than with Korean and Japanese pines.

However, the dendrogram obtained by NJM, and based on Cavalli-Sforza and Edwards' (1967) distance, D_{ch} , has revealed a kind of "intermediate" position of whitebark pine between two stone pine groups, Swiss and Siberian stone pines, on one hand, and Korean and Japanese stone pines, on the other (fig. 3). In these cases NJM gives more an intuitively realistic phylogenetic tree. It is important to note that both UPGMA dendrograms based on D_{ch} and Nei's distance, D , have practically the same topology, but they differ from the NJM dendrogram. Thus, one can conclude that assumption of equal evolutionary rates of stone pine species can be erroneous.

Millar and Kinloch (1991) discuss several theoretically possible variants of whitebark pine origin: (1) from ancestral Eurasian stone pine with penetration into North America during the Mesozoic (before Laurasia segregation), Tertiary, or Quarternary (through the Bering land bridge) time; (2) from one of the American pines of subsection *Strobi*. Now we can finally solve this problem. Nei's genetic distances (D) between whitebark pine and Eurasian stone pines equal approximately 0.121-0.256 (table 3). The time of divergence (t) between whitebark pine and Eurasian stone pines, theoretically estimated from these values, is 0.6-1.3 million years, using calibration coefficient (k) 5×10^6 in the equation $t = kD$ (Nei 1975; 1987a,b). This corresponds quite well to the approximate geological time of the Bering Strait opening—1.8-3.5 million years ago—estimated by different methods (see references in Grant 1987). Consequently, this event, the Bering Strait opening, can be, obviously, considered as the beginning of genetic differentiation between North American and Eurasian pines due to geographical isolation.

Thus, the hypothesis of a relatively recent penetration of ancient stone pines into North America through the Bering land bridge in the Pliocene seems most preferable. If we assumed the hypothesis that a more ancient penetration of stone pines through a "Euramerican" connection had occurred during Mesozoic time (Millar and Kinloch 1991), much more differentiation between whitebark pine and Eurasian stone pines should have been found in our study. The assumption of whitebark pine origin from *Strobi* pines must be rejected, according to our data, but phylogenetic relationships of stone pines with other relative species from subsections *Strobi* and *Cembroides* certainly need much more analysis. The first steps in this direction have been made recently using cpDNA markers.

Chloroplast DNA Data and Pine Phylogeny—Only a few studies on pine phylogeny using DNA markers have been made. This allows us to draw a short comparison of the Millar and Kinloch (1991) results with our data, presented here, paying special attention to phylogenetic relationships of stone pines with some other closely related species.

Chloroplast DNA (cpDNA) restriction fragment length polymorphism (RFLP) of the five stone pine species and four white pine species of a closely related subsection *Strobi*—limber pine, sugar pine (*P. lambertiana* Dougl.), western white pine (*P. monticola* Dougl.), and eastern white pine—have been recently studied by Krutovskii and Wagner (1993). Data have been obtained by molecular hybridization of 27

probes, representing the entire chloroplast genome of *P. contorta*, with restriction fragments from 20 endonucleases. The total number of restriction fragments per sample varied from 378 to 422.

Chloroplast DNA variation among trees within species was not pronounced ($D = 0.0-0.0013$) and was comparable with variation between populations within species, but cpDNA diversity, in general, was quite high—50 to 100 percent individual cpDNA belonged to different haplotypes (for more details see Krutovskii and Wagner 1993). The dendrogram constructed on Nei's genetic distances (D), estimated from these data (Nei 1987b; Nei and Miller 1990), has shown almost the same phylogenetic relationships between stone pine species as established on isozyme loci data (fig. 3). The stone and white pine species have been undoubtedly divided into two separate groups (fig. 4). It is interesting to note that NJM dendrograms give better correspondence between cpDNA and isozyme data. Comparing NJM and UPGMA dendrograms we can suppose that assumption of homogeneity of evolutionary rates is less proper for cpDNA than for nuclear (isozyme) genes.

The cpDNA data also indicate that genetic differentiation is more developed among the four *Strobi* species than

among the *Cembrae* species. The same conclusion has been made by Shurkhal and others 1991a,b; 1992) on the isozyme data.

Chloroplast DNA's of whitebark pine and Eurasian stone pine species were remarkably similar. This similarity, together with clear cpDNA divergence between the two subsections, confirms systematic classification of whitebark pine in subsection *Cembrae*, and not in subsection *Strobi*. Phylogenetic relationships of whitebark pine with Siberian and Swiss stone pines revealed by cpDNA RFLP analysis are surprisingly consistent with the conclusions from the analysis of 16 isozyme loci (fig. 3). Thus, our observation is not an artifact, because two independent sets of genetic markers (isozymes and cpDNA RFLPs) have produced the same conclusions. Moreover, Szmidt (1991) notes that the present geographic distribution of some forest tree species often shows little correlation with the degree of cpDNA differentiation among them, because the present geographic distribution of some species is of relatively recent origin.

The data obtained by Szmidt and others (1988), who used four restriction enzymes for cpDNA RFLP analysis of 12 pine species, including two stone pine species (Swiss stone and whitebark pines) and two white pine species (western

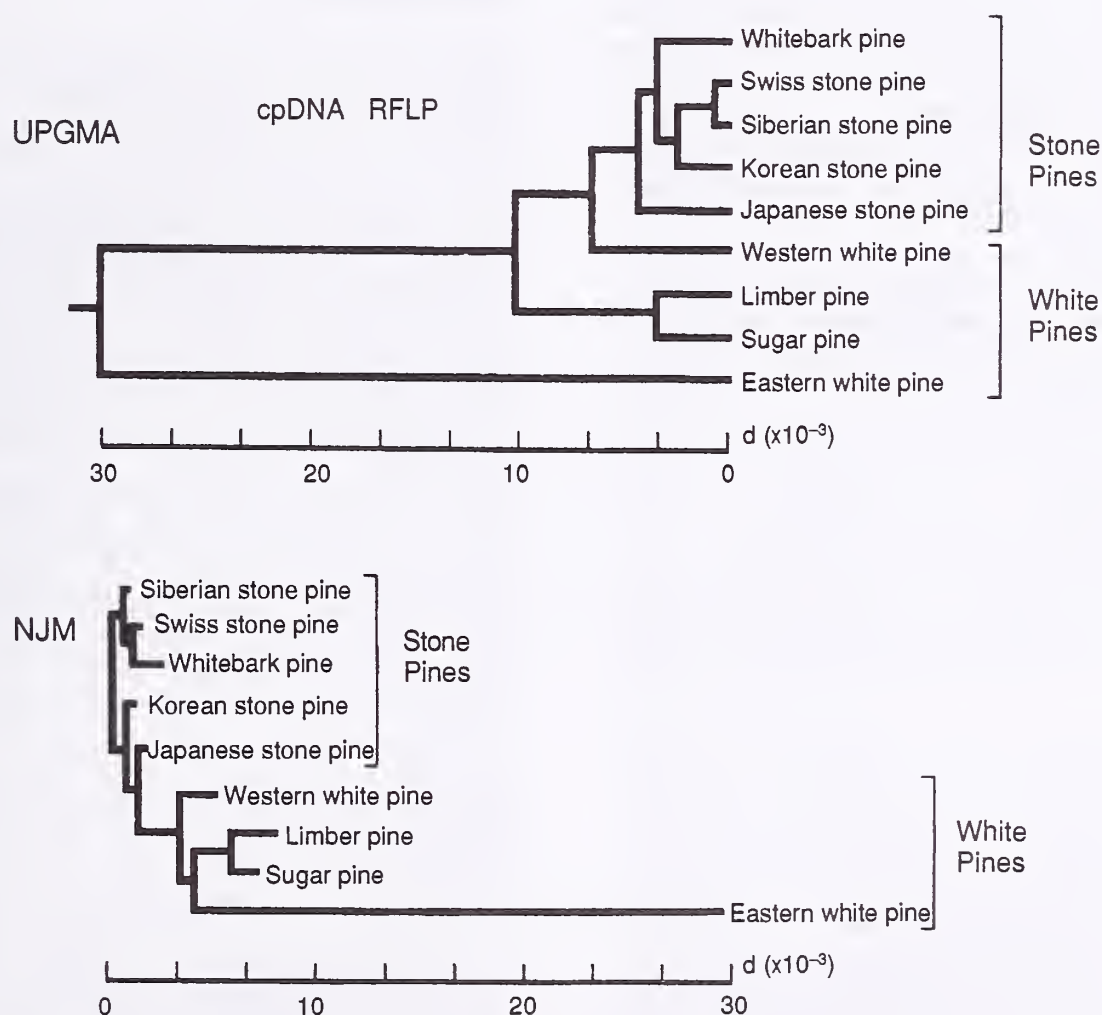


Figure 4—UPGMA and NJM dendrograms of five stone pine species (subsection *Cembrae*) and four white pine species closely related to them: *Pinus flexilis*, *P. lambertiana*, *P. monticola*, and *P. strobus* (subsection *Strobi*), based on Nei's genetic distances, d , (Nei 1987b; Nei and Miller 1990), and calculated from chloroplast (cp) DNA restriction fragment length polymorphism (RFLP) data (Krutovskii and Wagner 1993).

and eastern white pines), also confirm our results. They evaluated phylogenetic relationships between these species using UPGMA clustering based on dissimilarity index, analogous to Nei's D. According to the dendrogram given by Szmidt and others (1988), Swiss stone and whitebark pines form a very tight separate cluster. Western white pine is distantly linked to this cluster, which exactly corresponds to our data (fig. 4). Eastern white pine forms a separate branch but is closely linked to the group of Swiss stone, whitebark, and western white pines.

Analogous data have been obtained by Strauss and Doerksen (1990) who studied one sample from each of 18 to 19 pine species representing 14 to 15 subsections using eight restriction enzymes and 17 cloned DNA fragments (mostly from *Pseudotsuga menziesii*). At least 65 percent of the chloroplast genome was covered by the combination of the probes used. The samples have also included two stone pine species (Korean stone and whitebark pines) and two white pine species (blue and sugar pines). Distances between the samples were estimated via shared characters. The stone and white pine species were extremely similar to one another, with distances ranging from 0.0 to 0.018. They form one cluster. The authors have mentioned (data have not been presented) that other, more limited, restriction fragment studies of section *Strobus*, including three stone (Swiss, Siberian, and Japanese) and three white pines (Armand's [*P. armandii* Franch.], limber, and western white), have given the same indication of high uniformity. Unfortunately, Strauss and Doerksen (1990) have not been able to distinguish stone and white pines, probably because a limited number of restriction enzymes or DNA probes have been used in their research.

Certainly, stone pines and other closely related species need more genetic analysis using both isozyme and DNA markers. Many fascinating aspects of their evolution are sure to remain hidden, and many discoveries are still waiting for research.

CONCLUSIONS

The main conclusions based on our data are:

1. Both biochemical (isozymes) and molecular (cpDNA) genetic markers are very useful and informative for study of population genetic structure and phylogeny of stone pine and other closely related species, and they complement each other.
2. In spite of the high level of isozyme loci and cpDNA diversity among stone pine species, genetic differentiation between the populations is not pronounced, but specific. As a minimum, the genetic differentiation reflects their geographical and ecological peculiarities. Thus, it is necessary to study populations from the whole of the stone pine species area for careful description of gene distribution, taking into account even very small genetic differences between populations for developing gene conservation and reforestation programs.
3. According to both isozyme and cpDNA restriction fragment analyses, *P. albicaulis* undoubtedly belongs to *Cembrae* species and not to *Strobi* species.
4. Stone pine species consist of a compact group of very closely related and genetically similar species, obviously

having monophyletic origin, supposedly, from ancient Siberian stone pine. Thus, subsection *Cembrae* should be considered as a valid taxon.

ACKNOWLEDGMENTS

We are very grateful to V. N. Vorobjev and N. A. Vorobjeva (Institute of Ecology of Natural Complexes, Tomsk, Russia), L. I. Milyutin and his laboratory staff (Institute of Forest and Timber, Krasnoyarsk, Russia), G. R. Furnier (University of Minnesota, Minneapolis, MN, U.S.A.), R. T. Gut (Forest Technology Institute, Lvov, Ukraine), and P. Razumov (Far East Forest Institute, Khabarovsk, Russia) for their help in collecting and kindly providing *Cembrae* species seed samples for isozyme analysis. We are thankful to Yu. S. Belokon' (Institute of General Genetics, Moscow, Russia) for very helpful assistance in electrophoretic analysis, R. M. Lanner (Utah State University, Logan, UT, U.S.A.), D. F. Tomback (University of Colorado at Denver, Denver, CO, U.S.A.), and C. Millar (Institute of Forest Genetics, Berkeley, CA, U.S.A.) for very useful comments on pine phylogeny. We also appreciate H.-R. Gregorius' invaluable comments that helped to substantially improve the manuscript.

REFERENCES

- Altukhov, Y. P. 1990. Population genetics: diversity and stability. New York: Harwood Academic Publishers. 352 p.
- Altukhov, Y. P.; Krutovskii, K. V.; Dukharev, V. A.; Larionova, A. Y.; Politov, D. V.; Ryabokon', S. M. 1989. Biochemical population genetics of woody forest species. In: Iroshnikov, A. I., ed. International symposium on forest genetics, breeding and physiology of woody plants: proceedings; 1989 September 24-30; Voronezh. Moscow: The State Forest Committee of the USSR: 21-29.
- Bergmann, F. 1978. The allelic distribution of an acid phosphatase locus in Norway spruce (*Picea abies*) along similar climatic gradients. Theoretical and Applied Genetics. 24: 57-64.
- Bobrov, E. G. 1978. Forest-forming conifers of the USSR. Moscow: Nauka. 190 p. [In Russian].
- Carsey, K. S.; Tomback, D. F. 1992. Growth form distribution and genetic relationships in tree clusters of *Pinus flexilis*, a bird-dispersed pine. Oecologia. [In press.]
- Cavalli-Sforza, L. L.; Edwards, A. W. F. 1967. Phylogenetic analysis: models and estimation procedures. American Journal of Human Genetics. 19(2): 233-257.
- Conkle, M. T.; Schiller, G.; Grunwald, C. 1988. Electrophoretic analysis of diversity and phylogeny of *Pinus brutia* and closely related taxa. Systematic Botany. 13(3): 411-424.
- Crawford, D. J. 1983. Phylogenetic and systematic inferences from electrophoretic studies. In: Tanksley, S. D.; Orton, T. J., eds. Isozymes in plant genetics and breeding. Part A. Amsterdam: Elsevier Scientific Publishers: 257-287.
- Critchfield, W. B. 1986. Hybridization and classification of the white pines (*Pinus* section *Strobus*). Taxon. 35(4): 647-656.
- Critchfield, W. B.; Little, E. L. 1966. Geographic distribution of the pines of the world. Washington, DC: U.S. Department of Agriculture. 99 p.

- Dancik, B. P.; Yeh, F. C. 1983. Allozyme variability and evolution of lodgepole pine (*Pinus contorta* var. *latifolia*) and jack pine (*Pinus banksiana*) in Alberta. Canadian Journal of Genetics and Cytology. 25: 57-64.
- Farjon, A. 1984. Pines: drawings and descriptions of the genus *Pinus*. Leiden: E. J. Brill. 204 p.
- Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. American Naturalist. 106(951): 645-668.
- Furnier, G. R.; Adams, W. T. 1986. Geographic patterns of allozyme variation in jeffrey pine. American Journal of Botany. 73(7): 1009-1015.
- Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, B. P. 1987. Effect of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41(3): 607-612.
- Goncharenko, G. G.; Padutov, V. E.; Silin, A. E. 1992. Population structure, gene diversity, and differentiation in natural populations of cedar pines (*Pinus* subsection *Cembrae*, *Pinaceae*) in the USSR. Plant Systematics and Evolution. 182(3-4): 121-134.
- Gottlieb, L. D. 1977. Electrophoretic evidence and plant systematics. Annals of Missouri Botanical Garden. 64: 161-180.
- Grant, W. S. 1987. Genetic divergence between congeneric Atlantic and Pacific Ocean fishes. In: Ryman, N.; Utter, F., eds. Population genetics and fishery management. Seattle, WA: University of Washington Press: 225-246.
- Hamrick, J. L. 1983. The distribution of genetic variation within and among natural plant populations. In: Chambers, S.; Schonewald-Cox, C., eds. Genetics and wild population management. Reading, PA: Addison-Wesley: 335-349; 501-509.
- Hamrick, J. L.; Godt, M. J. 1989. Allozyme diversity in plant species. In: Brown, A. H. D.; Clegg, M. T.; Kahler, A. L.; Weir, B. S., eds. Plant population genetics breeding and genetic resources. Sanderland, MA: Sinauer Associates: 43-63.
- Hamrick, J. L.; Loveless, M. D. 1986. The influence of seed dispersal mechanisms on the genetic structure of plant populations. In: Estrada, J.; Fleming, T. H., eds. Frugivores and seed dispersal. Dordrecht, The Netherlands: Dr. W. Junk Publishers: 211-223.
- Hamrick, J. L.; Mitton, J. B.; Linhart, G. B. 1981. Levels of genetic variation in trees: influence of life history characteristics. In: Conkle, M. T., ed. Symposium on isozymes in North American forest trees and forest insects: proceedings. Berkeley, CA: U.S. Department of Agriculture, Forest Service: 35-41.
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P. 1987. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. I. Genetic control of isozyme systems. Genetika. 23(12): 2216-2228. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1988 June: 1568-1576].
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P. 1988. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. II. Level of allozyme variability in western Sayan. Genetika. 24(1): 118-124. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1988 July: 81-86].
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P.; Milyutin, L. I.; Kuznetsova, G. V.; Iroshnikov, A. I.; Vorobjev, V. N.; Vorobjeva, N. A. 1989. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. IV. Genetic diversity and differentiation between populations. Genetika. 25(11): 2009-2032. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1990 May: 1343-1362].
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P. 1990. Interspecific genetic differentiation of Eurasian stone pines for isoenzyme loci. Genetika. 26(4): 694-707. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1990 October: 440-450].
- Krutovskii, K. V.; Politov, D. V. 1992. Study of intra- and interspecific genetic differentiation between Eurasian cedar pines using isozyme loci and multidimensional analysis. In: Symposium on molecular mechanisms of genetic processes: proceedings. Moscow: Nauka Publishers: 87-96. [In Russian].
- Krutovskii, K. V.; Wagner, D. B. 1993. [Unpublished.] Chloroplast DNA variation and phylogeny in *Pinus* subsections *Cembrae* and *Strobi* (subgenus *Strobus*). Lexington, KY: University of Kentucky, Department of Forestry. [Working draft].
- Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: 6th North American Forest Biology Workshop: proceedings; 1980 August 11-13; Edmonton, AB. Edmonton, AB: University of Alberta: 15-47.
- Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12: 391-402.
- Lanner, R. M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.
- Litvintseva, M. V. 1974. Characteristics of needle parenchymal cell structure in species of the group *Cembrae* of the genus *Pinus*. Botanicheski Zhurnal. [Leningrad]. 59(10): 1501-1505. [In Russian].
- Little, E. L.; Critchfield, W. B. 1969. Subdivisions of the genus *Pinus* (pines). Res. Rep. 1144. Washington, DC: U.S. Department of Agriculture, Forest Service: 1-51.
- Loveless, M. D.; Hamrick, J. L. 1984. Ecological determinants of genetic structure in plant populations. Annual Review of Ecology and Systematics. 15: 65-95.
- Millar, C. I. 1983. A steep cline in *Pinus muricata*. Evolution. 32(2): 311-319.
- Millar, C. I.; Kinloch, B. B. 1991. Taxonomy, phylogeny, and coevolution of pines and their stem rusts. In: Hiratsuka, Y.; Samoil, J. K.; Blenis, P. V.; Crane, P. E.; Laishley, B. L., eds. Rusts of pine. Inf. Rep. NOR-X-317. Edmonton, AB, Canada: Northern Forestry Centre.
- Nei, M. 1972. Genetic distance between populations. American Naturalist. 106: 283-292.
- Nei, M. 1975. Molecular population genetics and evolution. New York: American Elsevier. 288 p.
- Nei, M. 1977. F-statistics and analysis of gene diversity in subdivided populations. Annals of Human Genetics. 41: 225-233.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics. 89: 583-590.

- Nei, M. 1987a. Genetic distance and molecular phylogeny. In: Ryman, N.; Utter, F., eds. Population genetics and fishery management. Seattle, WA: University of Washington Press: 193-223.
- Nei, M. 1987b. Molecular evolutionary genetics. New York: Columbia University Press. 512 p.
- Nei, M.; Miller, J. C. 1990. A simple method for estimating average number of nucleotide substitutions within and between populations from restriction data. *Genetics*. 125: 873-879.
- Politov, D. V. 1989. Allozyme polymorphism, genetic differentiation, and mating system in Siberian stone pine, *Pinus sibirica* Du Tour. Moscow: Institute of General Genetics, Russian Academy of Sciences. 190 p. Dissertation Thesis. [In Russian].
- Politov, D. V.; Krutovskii, K. V.; Altukhov, Yu. P. 1989. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. III. Linkage relationships among isozyme loci. *Genetika*. 25(9): 1606-1618. [In Russian]. [English translation published by Plenum Publishing Corp. in *Soviet Genetics*; 1990 March: 1053-1063].
- Politov, D. V.; Krutovskii, K. V. 1990. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. V. Analysis of mating system. *Genetika*. 26(11): 2002-2011. [In Russian]. [English translation published by Plenum Publishing Corp. in *Soviet Genetics*; 1991 May: 1309-1316].
- Politov, D. V.; Krutovskii, K. V.; Altukhov, Yu. P. 1992. Isozyme loci characteristics of gene banks of populations of cedar pines. *Genetika*. 28(1): 93-114. [In Russian]. [English translation published by Plenum Publishing Corp. in *Soviet Genetics*; 1992 July: 76-95].
- Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. In: *Studies in Genetics VII*. Publ. 7213. Austin, TX: University of Texas: 145-153.
- Rohlf, F. J. 1988. NTSYS-pc: numerical taxonomy and multivariate analysis system. New York: Exeter Publishing Ltd.
- Saitou, N.; Nei, M. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*. 4: 406-425.
- Schuster, W. S. F.; Mitton, J. B. 1991. Relatedness within clusters of bird-dispersed pine and the potential for kin interactions. *Heredity*. 67: 41-48.
- Shaw, G. R. 1914. The genus *Pinus*. Publ. Arnold Arboretum No. 5. Cambridge, MA: Riverside Press. 96 p.
- Shurkhal, A.; Podogas, A.; Zhivotovsky, L. 1991a. Genetic differentiation of 18 pine species on allozyme loci, genus *Pinus*, subgenus *Strobos* and *Pinus*. *Doklady Akademii Nauk SSSR*. 316(2): 484-488. [In Russian]. [English translation published by Plenum Publishing Corp. in *Doklady Biological Sciences*; 1991].
- Shurkhal, A.; Podogas, A.; Zhivotovsky, L. 1991b. Phylogenetic analysis of genus *Pinus* by allozyme loci: genetical differentiation of subgenus. *Genetika*. 27(5): 1193-1205. [In Russian]. [English translation published by Plenum Publishing Corp. in *Soviet Genetics*; 1991 November].
- Shurkhal, A.; Podogas, A.; Zhivotovsky, L. 1992. Allozyme differentiation in the genus *Pinus*. *Silvae Genetica*. 41(2): 105-109.
- Sneath, P. H. A.; Sokal, R. R. 1973. Numerical taxonomy. San Francisco: W. H. Freeman: 230-234.
- Steinhoff, R. J.; Joyce, D. G.; Fins, L. 1983. Isozyme variation in *Pinus monticola*. *Canadian Journal of Forest Research*. 13(6): 1122-1131.
- Strauss, S. H.; Doerksen, A. H. 1990. Restriction fragment analysis of pine phylogeny. *Evolution*. 44(4): 1081-1096.
- Strauss, S. H.; Bosquet, J.; Hipkins, V. D.; Hong, Y.-P. 1992. Biochemical and molecular genetic markers in bio-systematic studies of forest trees. *New Forests*. 6: 125-158.
- Swofford, D. L.; Selander, R. B. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *Journal of Heredity*. 72: 281-283.
- Szmidt, A. E. 1991. Phylogenetic and applied studies on chloroplast genome in forest conifers. In: Hattemer, H. H.; Fineschi, S.; Cannata, F.; Malvolti, E. V., eds. *Biochemical markers in the population genetics of forest trees*. The Hague, The Netherlands: SPB Academic Publishing: 185-196.
- Szmidt, A. E.; Sigurgeirsson, A.; Wang, X. R.; Hållgren, J. E.; Lindgren, D. 1988. Genetic relationships among *Pinus* species based on chloroplast DNA polymorphism. In: Hållgren, J.-E., ed. *Frans Kempe Symposium in Umeå on molecular genetics of forest trees: proceedings; 1988; Umeå, Sweden*. Umeå, Sweden: Swedish University of Agricultural Sciences: 33-47.
- Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Nitecki, N. H., ed. *Coevolution*. Chicago: University of Chicago Press: 179-223.
- Tomback, D. F.; Hoffmann, L. A.; Sund, S. K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-129.
- Tomback, D. F.; Holtmeier, F. K.; Mattes, H.; Carsey, K. S.; Powell, M. L. 1992. Tree clusters and growth form distribution in *Pinus cembra*, a bird-dispersed pine. Denver, CO: University of Colorado at Denver, Department of Biology. [Working draft].
- Tomback, D. F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology*. 4: 185-219.
- Wheeler, N. C.; Guries, R. P. 1982. Population structure, genetic diversity and morphological variation in *Pinus contorta* Dougl. *Canadian Journal of Forest Research*. 12(3): 595-606.
- Wheeler, N. C.; Guries, R. P. 1987. A quantitative measure of introgression between lodgepole and jack pines. *Canadian Journal of Botany*. 65: 1876-1885.
- Wheeler, N. C.; Guries, R. P.; O'Malley, D. M. 1983. Bio-systematics of the genus *Pinus*, subsection *Contortae*. *Biochemical Systematics and Ecology*. 11: 333-340.
- Yeh, F. C. H.; Cheliak, W. M.; Dancik, B. P.; Illingworth, K.; Trust, D. C.; Pryhitka, B. A. 1985. Population differentiation in lodgepole pine, *Pinus contorta* ssp. *latifolia*: a discriminant analysis of allozyme variation. *Canadian Journal of Genetics and Cytology*. 27(2): 210-218.

COEVOLUTIONAL ASPECTS OF STONE PINES AND NUTCRACKERS

Hermann Mattes

Abstract—Nutcrackers (*Nucifraga caryocatactes* and *N. columbiana*) have developed a strong mutualistic relationship to stone pines. Seeds of stone pines are the most important food for at least 9 months of the year and for raising the young. In addition to special adaptations on gathering, transporting, caching, and finding again the hoarded seeds, the whole annual cycle of the nutcracker's life (time of breeding and moulting), its mating system, and its habitat use are adjusted to the use of pine seeds.

Within the family of jays, magpies, and crows (Corvidae) many characteristics of preadaptive value for seed dispersal occur (Tomback and Linhart 1990; Turcek and Kelso 1968). Three corvid species have evolved a strong mutualistic system with pines: Clark's nutcracker (*Nucifraga columbiana*) and the pinyon jay (*Gymnorhinus cyanocephalus*) in North America and the European nutcracker (*Nucifraga caryocatactes*) in Eurasia. Comprehensive studies on food regime and seed dispersal were carried out by many authors (Bibikov 1948; Crocq 1990; Hayashida 1982, these proceedings; Marzluff and Balda 1992; Mattes 1978; Reijmers 1959; Saito 1983; Swanberg 1951; Tomback 1977; Vander Wall and Balda 1977, 1981). Coevolution in corvids and pines does not only refer to feeding and caching behavior, but the whole life cycle is adjusted to the use of the special food resource. This paper describes the process for the European nutcracker.

THE EUROPEAN NUTCRACKER

The annual life cycle (fig. 1) of the nutcracker is best looked at from August onward. Unripe seeds of the Swiss stone pine (cembra pine, *Pinus cembra*) are eaten by the nutcracker throughout August or even in July; thus, the bird will not miss the point when the seeds are fully developed. At this time the resin flow in the cone stops, and cone scales get loose. Now the seeds can be easily taken out of the cone, and the nutcracker begins gathering and caching seeds for winter supply. Pine seed gathering will last until all seeds have been harvested and almost no cones are left on the trees. Only twice within 19 years of investigation in the Engadine a cone crop lasted until the beginning of the following spring.

In the Alps, nutcrackers carry seeds of cembra pine over distances up to 15 km (including differences in altitude of at least 700 m) back to their territories. They carry 45

pine seeds per flight on an average; however, a maximum load of 134 cembra pine seeds has been found in the sublingual pouch of a nutcracker. Main morphological and ethological adaptations for seed use are:

- a long and pointed bill (fig. 2) that enables the bird to take seeds out of the cones as one would with tweezers (most other corvids have a hooked bill);
- a rist in the lower mandible allows the bird to fix and crack pine seeds, supported by a short-cut tongue;
- the sublingual pouch allows carrying a large quantity of seeds (fig. 3) without disturbing other functions of the bill;
- ability to test seed quality by means of seed color and resonance (by so-called bill-clicking).

SEED CACHES

The cached seeds provide the main food source for the nutcracker from November to April, and to a lesser degree until July. A single nutcracker stores more than 25,000 seeds. As yet it has not been clearly shown how the nutcracker can retrieve its seed caches. However, as can be concluded from observations in the field and in the laboratory, nutcrackers apparently remember each single cache (Tomback 1982, and others). Further, there are no specific features of caches, although nutcrackers obviously prefer to deposit seeds near border lines and any changes of surface structure. Experiments with the Clark's nutcracker by Kamil and Balda (1988) and Vander Wall (1982) showed that nutcrackers orient (navigate) optically, as expected, and additionally with a magnetic sense. Understanding cache findings, however, requires more detailed information, as nutcrackers detect caches even under a thick cover of snow. Balda and Kamil (1989) suggest an overall fuzzy optical navigation for finding caches. This would allow the birds to locate a cache even if there were distinctive changes, for example, in height of snow cover, broken branches, or fallen trees. It is still an open question how the bird can find caches under a snow cover of 20 cm and higher, getting very directly to the hoarded seeds. Snow tunnels of 130 cm (Burckhardt 1958) and about 300 cm (R. Stern, personal communication) were reported, and—what is most surprising—the nutcrackers did find the cached seeds. Crocq (1990) found the nutcrackers leaving their subalpine habitat when snow cover reached 170 cm on undisturbed surfaces.

It should be emphasized that nutcrackers dig successfully for their caches throughout winter until early spring. That guarantees sufficient food for the brood during that difficult time of the year. Nutcrackers must remember not only the sites of the caches but additionally those that already have been used. This doubles the efforts of

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Hermann Mattes is Professor of Landscape Ecology and Geography, Department of Geography, University of Münster, Germany.

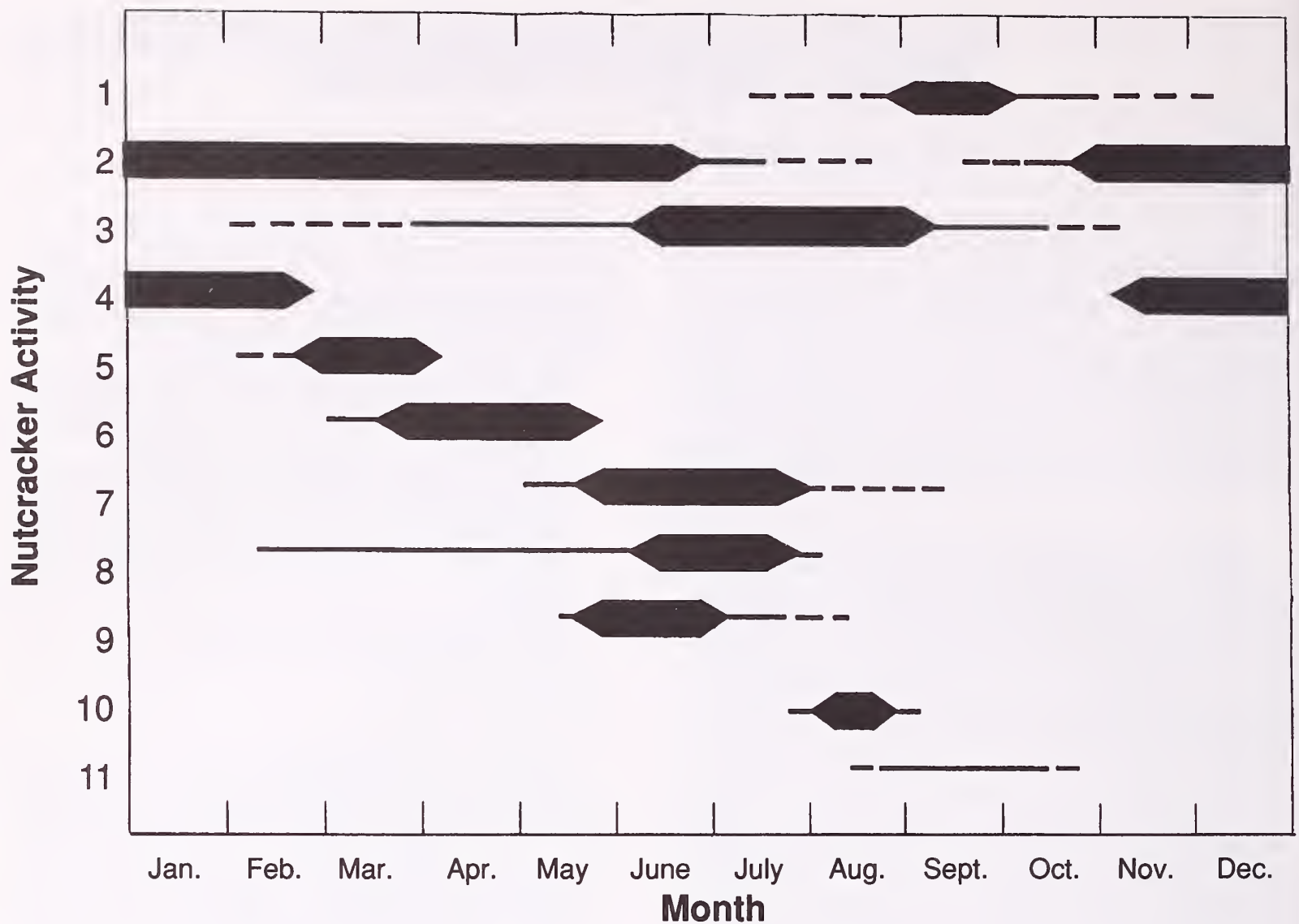


Figure 1—Annual activities of the nutcracker in the Alps for years with a medium cone crop. 1-3, feeding: 1, seed harvest and transport; 2, use of cached seeds; 3, consumption of animal food, for example, spiders, insects; 4, winter period; 5-7 breeding period: 5, courtship and nest building; 6, time with clutch and nestlings; 7, family groups with fledged young; 8-9, moulting: 8, moult of adults; 9, moult of fledglings; 10-11, movements: 10, dismigration; 11, migration.



Figure 2—Inside the nutcracker's bill: short split tongue, underneath opening of sublingual pouch with peanut in the entrance part, rictus in the lower mandible.

memory. There is some evidence that nutcrackers use caches from the penultimate seed crop, which may be important in case a cone crop fails. In years of small seed crops, nutcrackers often recache the seeds. Temporary caches are made in cases of strong competition for seeds (when great numbers of nutcrackers and squirrels concentrate on a few cone-bearing trees). In temporary caches, nutcrackers mostly hide cones.

BREEDING AND HABITAT

Nutcrackers start breeding in March (fig. 4). At this time mean daily temperature is under 0 °C. Early breeding is necessary because the next generation has to be ready for harvesting seeds in August to ensure the winter food supply. Breeding takes about 18 days, the nestlings fledge when 24 to 28 days old, and there is an extraordinarily long time of parental care for the fledglings—until they are about 100 days old (Oberauer 1991; Rudat 1978). Extensive care by the parents is needed because of scarcity



Figure 3—Nutcracker with filled sublingual pouch. Morteratsch, Engadin; September 1975.

of food up to mid-June, and to provide training for caching and digging for seeds.

Courtship behavior starts in the end of February or early March. Synchronizing with the partner is of extreme importance for successful breeding. By February the nutcrackers' so-called ceremonial gatherings begin and then can be frequently observed (Swanberg 1956). Up to 12 or more nutcrackers from neighboring and sometimes far territories meet in conspicuous noisy groups. An individually marked female nutcracker that had spent the winter outside its territory came back late—March 17. I discovered her fighting for the territory while a ceremonial gathering was going on. She succeeded in reoccupying her former place, and raised two nestlings after having a three-egg clutch with one unfertile and half-sized egg. Neighbors know each other individually. So, except in artificially created feeding places, fights are very rare.

Nutcracker territories are organized in a different way than those of other passerines. Only the area very close to the nest is defended against intruders and thus can be called "territory" in the usual sense. In a broader sense, the territory comprises the area of food caches and is about 5 to 12 ha large according to habitat. These "territories" can overlap and are not defended because cached seeds are only accessible to the very same nutcracker. In addition, all places regularly visited for seed gathering and transport should be regarded as home range. Habitats of the nutcracker are characterized by evergreen conifers. In such forests sheltered nesting places are available, and because snow cover is low under dense tree canopies cached seeds can be easily recovered.

Nutcrackers are adapted in many ways for breeding under winter conditions. The nest is heavily built with a layer of dry decayed wood for insulation against low temperature. Beginning with the first egg, the parents must warm the clutch without long interruptions. Breeding starts after the last egg has been laid, and egg temperature is raised from about 25 °C to breeding conditions of about 38 °C. Different from most corvids, both adults breed. The male develops a large breeding patch, too. The female's breeding time is somewhat higher during the day, and it also stays on the nest at night. The nestlings are fed with pine seeds from their first day of life. Additional food consists of spiders, and, if available, insects. Nutrient analysis in seeds of whitebark pine (*Pinus albicaulis*) by Lanner and Gilbert (these proceedings) showed a high nutritive quality in caloric value, mineral nutrients, fatty acids, and amino acids. Should this apply also to cembra pine seeds, it is easy to understand why first-day nestlings can live mainly on a seed diet.

For successful overwintering and reproduction, sufficient numbers of seed caches must be available to both parents. First-year birds dismigrate in August and establish their own territory when seed caching starts. First-year birds that are not fully developed until August will have a minor chance to survive winter. A few first-year birds leave their native area in September and migrate in southern directions (Mattes and Jenni 1984). Adult nutcrackers are highly sedentary. Nonbreeding individuals might have action ranges within or between the territories of breeding birds. This population reserve can compensate for winter losses of adult birds.

In the "Stazer Wald" I observed a third bird helping a pair build their nest; unfortunately, no further observation was possible. Similar to several jay species, helping in breeding may be an evolutionary feature in the nutcracker (Woolfenden and Fitzpatrick 1984). Nutcrackers live monogamously for life, as can be concluded from individually marked birds (Mattes 1978; Swanberg 1956). In



Figure 4—A nutcracker breeding, the nest completely covered by snow. March 19, 1975, Engadin.

the Engadine, the mortality rate in adult birds was 84 percent (Mattes, in preparation) on an average. The oldest birds found were at least 15. Keeping territories and partners for life supports synchronization of the parents, and individual knowledge of neighbors minimizes social competition. Social hierarchy is evident and most conspicuous at artificial feeding places. Females take over the social rank of their mates (Grabher-Meyer 1991).

In passerines, moult normally takes place after the breeding season. Prolonged care of the fledglings and beginning of seed hoarding in August would not leave time for moulting in late summer. Actually, moult starts in March with change of remiges and tail feathers, and ends in July when body feathers are changed. Moult completely parallels breeding season; the double physiological effort causes a very long moulting period. Body feathers are moulted relatively quickly during the warmest part of the year.

REACTION TO CHANGES

Predation on pine seeds has influenced the whole life cycle of the nutcracker. Many features common to the corvids are particularly developed in the nutcracker. Still there is a broad and flexible reaction to environmental changes. This is most apparent during the invasions of Siberian nutcrackers (*N. c. macrorhynchos*) into western Europe. Diet and feeding as well as habitat use vary widely. Nevertheless, most of the invading birds very likely die. Some, however, return to their breeding ground either in the current autumn or in the next spring. Numerous birds ringed in the Åland archipelago (Finland) in August 1968 were recaptured a few weeks later in the East; three birds were found beyond the Urals at a maximum distance of almost 3,000 km (Zink 1981). Invaders stayed at wintering places in Bielefeld, Germany, when Siberian pine seeds (*Pinus sibirica*) were offered ad libitum (Conrads and Balda 1979).

Outside the natural range of cembra pine (Central Alps, Tatra, and a few locations in the Carpathian mountains) the European nutcracker normally feeds on hazel nuts (*Corylus avellana*). Slight, but statistically significant, differences in bill size are apparent in central-alpine populations. Nutcrackers from the Engadine and migrating birds at Col de Bretolet in southwestern Switzerland show a narrower lower mandible and a longer bill compared with populations from southern Germany and from northern Europe (Mattes 1978; Mattes and Jenni 1984). Also, there are distinct differences in bill size in populations of *N. c. macella* from Szetchuan and from Sikkim (Mattes, unpublished). Generally, there seems to be a correlation of width of lower mandible and size of main food. The distance between the branches of the lower mandible limits the size of the entrance to the sublingual pouch. As the main food of most Asian populations of the nutcracker is not yet sufficiently known, bill size and bill structure cannot yet be fully explained. Furthermore, bill size in some subspecies may reflect feeding conditions at former times.

REFERENCES

- Balda, Russel P.; Kamil, Alan C. 1989. A comparative study of cache recovery by three corvid species. *Animal Behavior*. 38: 486-495.
- Bibikov, D. I. 1948. On the ecology of the nutcracker. *Trudy Pechoro-Ilychko Gosud. Zapovednik*. 4: 89-112.
- Burckhardt, D. 1958. Vom Vorratanlegen des Tannenhähers. *Bündnerwald*. 11:102-114.
- Conrads, Klaus; Balda, Russell P. 1979. Überwinterungschancen Sibirischer Tannenhäher (*Nucifraga caryocatactes macrorhynchos*) im Invasionsgebiet. *Bericht des Naturwissenschaftlichen Vereins Bielefeld*. 24: 115-137.
- Crocq, Claude. 1990. *Le casse-noix mouchete (Nucifraga caryocatactes)*. Paris: Lechevalier/R. Chabaud. 326 p.
- Grabher-Meyer, Arno. 1991. Beobachtungen zur Brutbiologie einer kleinen Population des Tannenhähers (*Nucifraga caryocatactes*) bei Praxmar, Sellrain. Diplomarbeit, Universität Innsbruck, Austria.
- Kamil, Alan C.; Balda, Russell P. 1988. Spatial memory in Clark's nutcracker (*Nucifraga columbiana*). *Acta XIX Congressus Internat. Ornithol.*, Ottawa 1986. Vol. II: 2100-2111.
- Lanner, Ronald M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. *Canadian Journal of Forest Research*. 12(2): 391-402.
- Marzluff, John M.; Balda, Russ P. 1992. The pinyon jay: behavioral ecology of a colonial and cooperative corvid. London: Poyser. 317 p.
- Mattes, Hermann R. 1978. Der Tannenhäher im Engadin. Studien zu seiner Ökologie und Funktion im Arvenwald. *Münstersche Geographische Arbeiten* 2. Paderborn: Schöningh. 87 p.
- Mattes, Hermann R.; Jenni, Lukas. 1984. Ortstreue und Zugbewegungen des Tannenhähers (*Nucifraga caryocatactes*) im Alpenraum und am Randecker Maar/Schwäbische Alb. *Ornithologischer Beobachter*. 81: 303-315.
- Oberauer, Eva. 1991. Zur Postembryonalentwicklung des Tannenhähers (*Nucifraga caryocatactes* L.). Beobachtungen im Alpenzoo Innsbruck. Diplomarbeit, Universität Innsbruck, Austria. 140 p.
- Reijmers, N. F. 1959. Birds of the cedar-pine forests of south-central Siberia and their role in the life of the cedar-pine. *Trudy biolog. Inst. sibirsk. Otdel. Akad. Nauk SSSR*. 5: 121-166.
- Rudat, Volker; Rudat, Wolf. 1978. Zum Verhalten von Tannenhäherfamilien (*Nucifraga caryocatactes* L.) in der Zeit vom Ausfliegen der Jungen bis zu deren Selbständigwerden. *Zoologisches Jahrbuch für Systematik*. 105: 386-398.
- Saito, Shin-ichiro. 1983. On the relations of the caching by animals on the seed germination of Japanese stone pine, *Pinus pumila* Regel. *Bulletin of the Shiretoko Museum*. 5: 23-40.
- Swanberg, Peer O. 1951. Food storage, territory and song in the thickbilled nutcracker. *Acta X Congressus Internat. Ornitholog.* Uppsala 1950: 545-554.
- Swanberg, Peer O. 1956. Territory in the thickbilled nutcracker (*Nucifraga caryocatactes*). *Ibis*. 98: 412-419.

- Tomback, Diana F. 1977. Foraging strategies of Clark's nutcracker. *The Living Bird*. 17: 123-161.
- Tomback, Diana F. 1982. How nutcrackers find their seed stores. *The Condor*. 82: 10-19.
- Tomback, Diana F.; Linhart, Yan B. 1988. The evolution of bird-dispersed pines. *Evolutionary Ecology*. 4: 185-219.
- Vander Wall, Stephen B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. *Animal Behavior*. 30: 84-94.
- Vander Wall, Stephen B.; Balda, Russ P. 1977. Coadaptations of the Clark's nutcracker and the pinyon pine for efficient seed harvest and dispersal. *Ecological Monographs*. 47(1): 27-37.
- Vander Wall, Stephen B.; Balda, Russ P. 1981. Ecology and evolution of food storage behavior in conifer-seed-caching Corvids. *Zeitschrift für Tierpsychologie*. 56: 217-242.
- Woolfenden, D. E.; Fitzpatrick, W.-J. 1984. *The Florida scrub jay*. Princeton, NJ: Princeton University Press.
- Zink, Gerhard. 1981. *Der Zug europäischer Zugvögel*. 3. Lieferung. Möggingen: Vogelzug-Verlag.

ALLOZYME POLYMORPHISM, HETEROZYGOSITY, AND MATING SYSTEM OF STONE PINES

Dmitri V. Politov
Konstantin V. Krutovskii

Abstract—Population genetic structure and the mating system of stone pines (genus *Pinus*, subsection *Cembrae*) have been studied using isozymes. Observed were a tendency to heterozygote deficiency among embryos (obviously, a consequence of self-pollination with the estimated frequency of 0.11-0.30) and a slight heterozygote excess in adult trees (probably caused by selection against inbred progeny and balanced selection).

Electrophoretic analysis of allozyme polymorphism is one of the most useful methods for study of genetic and evolutionary processes in natural populations and taxonomic and phylogenetic relationships of forest tree species (Adams and others 1992; Fineschi and others 1991; Muller-Starck and Ziehe 1991). Conifers are particularly attractive, from a genetic point of view, because of their haploid megagametophyte (endosperm). Electrophoresis of both haploid and diploid (embryo) seed tissues permits us to distinguish maternal and paternal contributions into the progeny genotype. This makes it possible to estimate allele frequencies separately in both male and female gametes pools and to study segregating ratios directly by analyzing endosperm haplotypes, which correspond to haplotypes of female gametes. The possibility of observing meiotic products directly through study of haploid endosperms simplifies analysis of allozyme inheritance, genetic linkage of isozyme loci, and the mating system of conifers.

In contrast to many widespread European and North American conifer species, stone pines have been studied using isozymes only recently (Goncharenko and others 1988; Krutovskii and Politov 1992; Krutovskii and others 1987, 1988, 1989, 1990; Podogas and others 1991; Politov 1989; Politov and Krutovskii 1990; Politov and others 1989, 1992; Szmidi 1982). Meanwhile, the need for such data is apparent both for practical forestry applications and for purposes of genetic diversity conservation. As a major forest-forming tree species, stone pines determine, to a large extent, the state of ecosystems over extensive areas. Their genetic vulnerability thus threatens the existence of a unique forest type.

Four of the five stone pine species traditionally united in subsection *Cembrae* of genus *Pinus* (Critchfield and Little 1966) are found in Russia and neighboring countries: Siberian stone pine (*Pinus sibirica* Du Tour), European or Swiss stone pine (*P. cembra* L.), Korean pine (*P. koraiensis* Siebold et Zucc.), and mountain or Japanese stone pine (*P. pumila* [Pall.] Regel). All of them are very important economically.

This paper reports the main results of long-term population genetic studies on these species using isozyme analysis. Some population structure parameters also have been estimated for one population of whitebark pine (*P. albicaulis* Engelm.), the only representative of stone pines in the Western Hemisphere.

MATERIALS AND METHODS

Sampling Sites—Seeds collected in natural populations served as a source of laboratory material. *Pinus sibirica* seeds were collected from 11 localities. Samples designated as Filin Klyuch (F), Mutnaya Rechka (M), Malyi Kebezh (MK), Sobach'ya Rechka (SR), and Listvyanka (L) originate from the Western Sayan (Ermakovskii District, Krasnoyarsk Territory); Yayl'u (YA) from the Altai Mountains (Gorno-Altayskaya Autonomous Region); Smokotino (S), Zorkal'tsevo-1 (Z-1), and Zorkal'tsevo-3 (Z-3) from Tomskaya Region; Turukhan (TU) from the north of Krasnoyarsk Territory (Turukhanskii District); and N'alino (NYA) from the Khanty-Mansiiskii Autonomous District (Tyumenskaya Region). Besides, one locality of *P. cembra*, Ust'-Chornaya (UCH) from the Eastern Carpathians (Ukraine); three localities of *P. pumila* from the north of Kamchatka Peninsula designated as Grustnyi (GR), Uttyveem (UT), and Kamenskoye (K); and three localities of *P. koraiensis* from Khabarovsk Territory designated Malokhekhtsirskoye (MKH) and Khor (KHO), and from Primorskii Territory (Sikhote-Alin' (SA)) have been also studied. The sample of *P. albicaulis* originates from the Livingstone Falls (LF) population (southwestern Alberta, Canada).

Electrophoresis and Data Processing—No less than seven endosperms and embryos per tree have been studied using starch gel electrophoresis. Totally, 536 trees of five species (from 11 to 75 trees per population) and more than 3,500 embryos (7 to 20 per tree), as well as two bulked samples of seeds representing a large number of trees (TU and NYA), have been analyzed. Specimen preparation, buffer systems used, genetic interpretation of zymograms, and designations of allozymes, alleles, and loci have been described elsewhere (Krutovskii and others 1987; Politov 1989).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Dmitri V. Politov is Research Scientist and Konstantin V. Krutovskii is Senior Research Scientist, Laboratory of Population Genetics, Russian Academy of Sciences, Gubkin Str. 3, 117809 GSP-1 Moscow, Russia.

Genotypes of particular trees were inferred from segregation of alleles among their endosperms. Then, allele and genotype frequencies in samples of both mature trees and embryos, as well as in the effective pollen pool (paternal alleles of embryos), were estimated. Embryo tissue electrophoresis does not give high resolution for all zones of activity and, therefore, calculations based on embryo samples have included a smaller number of loci. Besides, some activity zones in individual species could not be reliably interpreted or were invariant. Because of this, specific sets of loci used for particular purposes in these species may differ somewhat. More detailed description of statistic procedures can be found elsewhere (Krutovskii and others 1989; Politov 1989; Politov and Krutovskii 1990; Politov and others 1989).

GENETIC CONTROL OF ISOZYMES AND LINKAGE OF LOCI

We have described inheritance of 11 isozyme systems of stone pines in our previous publications (Krutovskii and others 1987; Politov 1989) and found that they are controlled by at least 26 loci. However, only 21 most reliable loci with unambiguous genetic control have been included in this study (table 1). Segregation ratios of allelic variants of individual allozyme loci observed among endosperms of heterozygous trees correspond, with several exceptions, to the expected ones (1:1).

Analysis of joint allelic segregation for pairwise loci combinations in *Pinus sibirica* has revealed genetic linkage of loci Adh-1 and Lap-3 (with the mean recombination frequency 0.275), Adh-1 and Pgi-2 (0.301), and Fe-2 and Lap-2 (0.309). These loci belong to two linkage groups: Lap-3—Adh-1—Pgi-2 and Lap-2—Fe-2 (Politov and others 1989). Comparison of these data with those available in literature shows that stone pines, as well as other representatives of the family *Pinaceae*, are characterized by extreme conservatism of their genome, since the same loci combinations with nearly the same values of recombination frequency have been described not only in the closely related *P. albicaulis* (Furnier and others 1986), but also in many hard pines (see, for example, Szmidt and Muona 1989). Data presented here are apparently the first attempt of genetic mapping in one of the stone pines. However, one can assume that the linkage groups revealed in *P. sibirica* will also be found in other related species. Information of this kind could be useful for breeding programs, for analysis of association of genetic markers with economically important characters, and for mating system parameters estimation by multilocus methods.

POPULATION GENETIC STRUCTURE

Levels of Intrapopulation Variability—According to the gene diversity parameters estimated in stone pine populations using isozyme loci, the level of genetic variability appears to be rather high (table 2). There are almost no differences between observed heterozygosities and those expected from corresponding Hardy-Weinberg proportions. The values of the latter for individual species are: for *P. sibirica*—from 0.140 to 0.176, *P. cembra*—0.109,

Table 1—Enzymes and loci analyzed

Enzyme (abbreviation)	Total number of loci	Scored loci
Alcohol dehydrogenase (ADH)	2	Adh-1, Adh-2
Diaphorase (DIA)	3	Dia-1, Dia-2
Fluorescent esterase (FE)	3	Fe-2
Glutamate dehydrogenase (GDH)	1	Gdh
Glutamatoaloacetate transaminase (GOT)	3	Got-1, Got-2, Got-3
Isocitrate dehydrogenase (IDH)	1	Idh
Leucine aminopeptidase (LAP)	3	Lap-2, Lap-3
Malate dehydrogenase (MDH)	4	Mdh-1, Mdh-2, Mdh-3, Mdh-4
Phosphoglucose isomerase (PGI)	2	Pgi-2
Phosphoglucomutase (PGM)	2	Pgm-1, Pgm-2
Shikimate dehydrogenase (SKDH)	2	Skdh-1, Skdh-2

P. pumila—from 0.239 to 0.258, *P. koraiensis*—from 0.113 to 0.148, *P. albicaulis*—0.204.

Such a high amount of intrapopulation variability is characteristic of conifers. We have summarized data on allozyme diversity of 30 pine species using available references (Politov and others 1992). The mean number of alleles per locus (A) and the expected heterozygosity (H_e), averaged for all pine species, equalled 2.08 and 0.169, correspondingly. Comparable values have been found for spruces ($A = 2.2$, $H_e = 0.183$), larches ($A = 1.6$, $H_e = 0.091$), and representatives of other less-studied genera.

Factors supposedly promoting a high level of genetic diversity in stone pine populations include such ones, common for forest trees, as predominantly outcrossing mating system, wide distribution, large effective size of population, and high longevity (Hamrick and Godt 1989; Ledig 1986). More specific evolutionary factors, such as drastic reduction of population size ("bottleneck effect"), may also affect the variability level. Although the ranges of stone pines, both in Eurasia and in North America, were reduced during the Quaternary glacials (and also during the global warming), preservation of extensive refugia permitted avoidance of substantial genetic depauperization. This concerns *Pinus cembra* to a much less degree than other stone pines.

According to some evidence, Swiss stone pine underwent a sharp reduction in its range and population size during the Holocene caused by the global warming (Bobrov 1978 and references therein). A small effective number is typical of most populations of this species at present as well. Swiss stone pine exists nowadays in the Alps and the Carpathians as small isolated stands in which processes of genetic drift do not allow allozyme variability to be maintained on a high level. This is a most probable cause for a lower level of heterozygosity (0.109) and the percentage of polymorphic loci (26.3 percent) of *P. cembra*, as compared to other species. However, it should be noted, that the only sample of this species studied by us represents a small marginal stand from the eastern Carpathians, while central populations may appear to be more variable. The limited number of loci studied in the only work (Szmidt 1982) dealing with allozyme polymorphism in Swiss stone pine over the species

Table 2—Levels of allozyme variability in stone pine populations

Species and population names	Number of loci	Number of trees	A ¹	P ²	H _o ³	H _e ⁴
<i>Pinus sibirica</i>						
Filin Klyuch ⁵ (F ⁶)	19	53.0	1.8	47.4	0.155	0.152
Mutnaya Rechka (M)	19	75.0	1.9	47.4	.137	.140
Malyi Kebezh (MK)	19	15.0	1.8	52.6	.158	.153
Sobach'ya Rechka (SR)	19	12.0	1.7	42.1	.145	.173
Listvyanka (L)	19	41.0	1.9	42.1	.163	.151
Yayl'u (YA)	19	43.0	1.9	47.4	.153	.154
Smokotino (S)	19	43.0	1.7	42.1	.168	.161
Zorkal'tsevo-1 (Z-1)	19	34.0	1.7	47.4	.198	.176
Zorkal'tsevo-3 (Z-3)	19	34.0	1.7	47.4	.184	.165
Mean	19	38.9	1.8	46.2	.162	.158
<i>Pinus cembra</i>						
Ust'Chornaya (UCH)	19	15.0	1.5	26.3	.128	.109
<i>Pinus pumila</i>						
Grustnyi (GR)	20	54.0	2.3	50.0	.230	.239
Utyveem (UT)	20	55.0	2.5	60.0	.243	.251
Kamenskoye (K)	20	55.0	2.3	70.0	.269	.258
Mean	20	54.7	2.4	60.0	.247	.249
<i>Pinus koraiensis</i>						
Malokhekhtsirskoye (MKH)	17	30.0	1.6	47.1	.147	.132
Khor (KHO)	17	16.0	1.6	47.1	.162	.148
Sikhote-Alin' (SA)	17	11.0	1.5	35.3	.102	.113
Mean	17	19.0	1.6	43.2	.137	.131
<i>Pinus albicaulis</i>						
Livingstone Falls (LF)	16	52.0	1.9	56.3	.213	.204

¹Mean number of alleles per locus.²Mean percent of loci polymorphic (locus has been considered polymorphic if the frequency of the most common allele has not exceeded 95 percent).³Mean heterozygosity observed.⁴Mean heterozygosity expected.⁵See text for origins of populations.⁶Abbreviated denomination of population.

range does not allow any conclusions to be made about the variability level.

Heterozygosity of Korean pine (mean 0.131) is slightly higher. As to *Pinus pumila*, this species shows the highest values of H among stone pines (0.249), close to the maximum ones known for conifers (Politov and others 1992). One cannot exclude the fact that such a high variability is very important for adaptation of this species to a wide spectrum of environmental conditions, including those of permafrost regions, and drastic seasonal climatic changes. Nearly the same heterozygosity level (0.204) was found in the only studied population of whitebark pine from the north mountain area.

Genotype Distribution in Adult Trees and

Embryos—Comparison of observed genotype distributions with those expected from the corresponding Hardy-Weinberg proportions is commonly used in population genetics to reveal and identify various factors affecting genetic structure of populations. In stone pines such analysis has not revealed pronounced deviations from Hardy-Weinberg equilibrium for mature trees in any samples.

Statistically significant excess or deficiency of heterozygotes have not been observed for allozyme loci studied in stone pine populations. Nevertheless, the sign criterion showed that there were significantly more cases of a slight heterozygote excess (Politov and others 1992), which may mean existence of a tendency toward systematic excess of heterozygotes of allozyme loci among adult trees. Figure 1 shows mean values of Wright's fixation index (or "inbreeding coefficient," $F = 1 - H_o/H_e$, where H_o and H_e are mean observed and expected heterozygosities for all loci studied in the species). Predominance of slightly negative or almost zero F values indicates absence of significant heterozygote deficiency in the reproductive part of the populations. Species mean values were: for *P. sibirica*, -0.025; for *P. cembra*, -0.174; for *P. koraiensis*, -0.046. F values for *P. pumila* were slightly positive in two samples and negative in the third one (mean F = 0.008).

In most embryo samples, on the contrary, a slight deficiency of heterozygotes was regularly observed (Politov and others 1992). Figure 2 presents mean F values in embryos and adult trees calculated for the same loci. In embryos

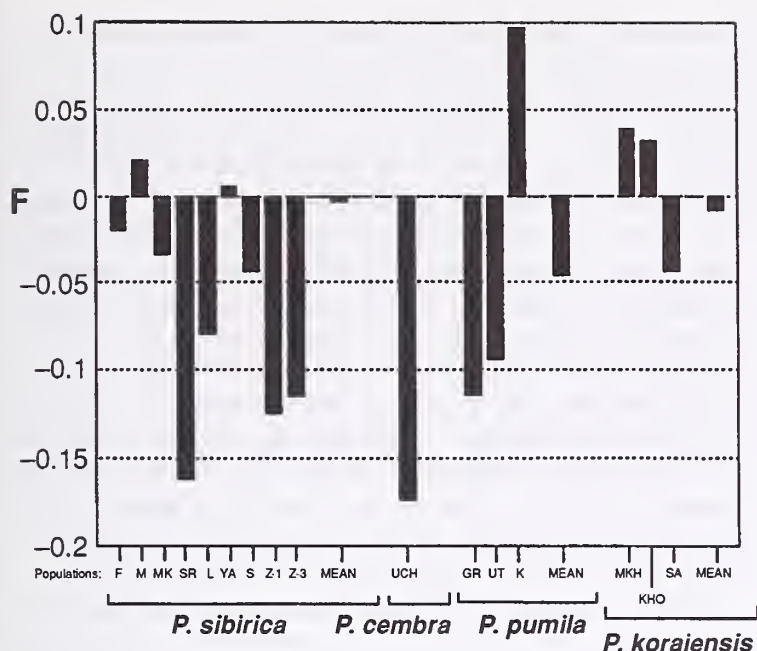


Figure 1—Observed fixation index (“inbreeding coefficient”) values (F) in samples of adult trees. All studied loci used. (For full names and origins of populations see text and table 2).

the values are positive in nearly all samples (except one), whereas mature trees display mainly negative F values.

Probable Causes of Heterozygote Deficiency—A most probable cause for heterozygote deficiency at early developmental stages of stone pines may be inbreeding. The species studied, as well as other conifers, have a mixed mating system (Brown and others 1985; Politov and Krutovskii 1990 and references therein) characterized by a random outcrossing with a certain percentage of selfing. Heterozygote deficiency may theoretically be caused by both self-pollination and other consanguineous matings (Ritland and El-Kassaby 1985; Shaw and others 1981). One cannot also exclude the action of natural selection against heterozygotes at a certain developmental stage.

Much evidence has been reported demonstrating heterozygote deficiency among embryos in populations of conifers (summarized by Bush and Smouse, 1992). In some rare cases deficiency is revealed in mature trees. The authors explained this phenomenon by inbreeding and, particularly, by selfing.

Mating System Analysis—The fact that selfing is most commonly regarded as a factor causing inbreeding in conifer species has good reasons. Coincidence, in general, of pollination with pistil receptivity of the same tree and absence of effective self-sterility mechanisms make this process highly probable. In order to test the hypothesis that partial selfing is the main cause of heterozygote deficiency in stone pines, we have applied methods of mating system parameters estimation based on allozyme data and mixed mating system theory (Brown and others 1985). Use of isozymes and powerful mathematical procedures (Expectation-maximization method, Newton-Raphson method, bootstrap, etc.) have made it possible to obtain quantitative estimates of selfing and outcrossing rates in natural conifer populations. For different species percentage of selfing varies between 2 to 3

and 20 to 30 percent (see Brown and others 1985; Politov and Krutovskii 1990, for review). For stone pines such estimates have not been made until recently. Here we present data obtained on three stone pine species.

The results of mating system analysis of Siberian stone pine have been published earlier (Politov and Krutovskii 1990). If we consider a randomly outcrossing population at equilibrium, absence of pre- and postzygotic selections, sexual symmetry, separated generations, etc., the expected inbreeding coefficient F_e can be derived from the equation $F_e = (1-t)/(1+t)$, where t is the outcrossing rate estimated for this species. In our study the expected inbreeding coefficient F_e has turned out to be very close to the actually observed one (F_o) [$F_o = (H_e - H_o)/H_e$, where H_e and H_o are, correspondingly, the expected from Hardy-Weinberg proportions and the directly observed heterozygosities] in embryo samples. Thus, selfing $(1-t)$ whose estimated rate is, on the average, as high as 15 percent (from 2 to 27 in individual populations) is most likely to be one of the main factors of heterozygote deficiency occurrence among embryos of this species.

Available data for three stone pine species are presented in table 3. Estimation of outcrossing rates was made based on four to eight polymorphic loci and using two different computation procedures—variants of both single- and multi-locus methods (Ritland and El-Kassaby 1985; Ritland and Jain 1981). Both procedures have been realized by Ritland (1990) in his original computer program MLT. The multi-locus estimation (which has more detective power than the single-locus one) gives for *Pinus sibirica* populations values ranging from 0.846 to 0.980 (mean 0.894), and for *P. koraiensis* values from 0.920 to 1.034 (mean 0.974). The outcrossing rate found in *P. cembra* was substantially lower

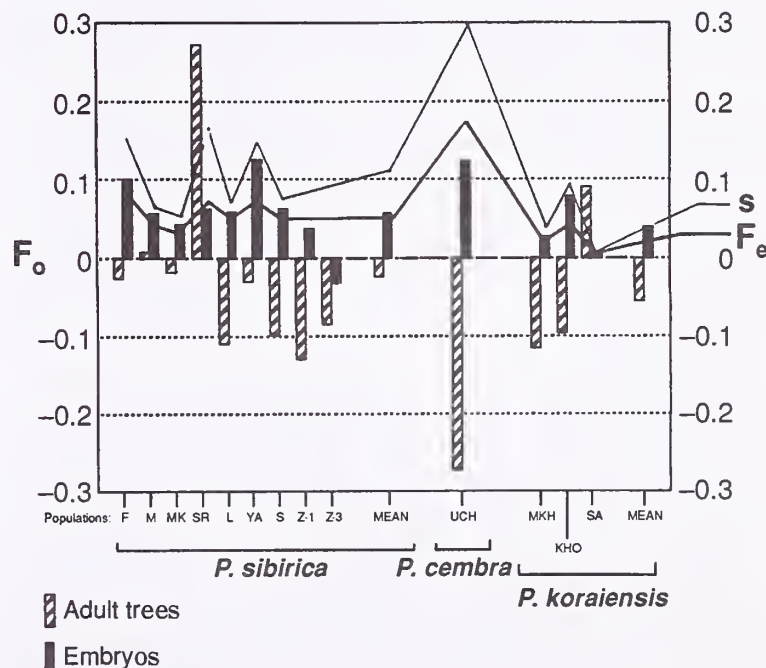


Figure 2—Observed fixation index, “inbreeding coefficient” (F_o), values in samples of adult trees (striped bars) and embryos (filled bars). Only eight common loci used. F_e is expected inbreeding coefficient [$F_e = (1-t_m)/(1+t_m)$]. s is selfing rate ($s = 1-t_m$, see table 3). (For full names and origins of populations see text and table 2).

Table 3—Multilocus (t_m) and single-locus (t_s) estimates of outcrossing rate in stone pine populations

Species and population names	Number of loci	Outcrossing rate			
		t_m (s.e.)		t_s (s.e.)	
<i>Pinus sibirica</i>					
Filin Klyuch-85 ¹	8.0	0.817	(0.031)	0.788	(0.030)
Filin Klyuch-86	8.0	.892	(.042)	.884	(.052)
Mutnaya Rechka-86	8.0	.980	(.019)	.959	(.048)
Mutnaya Rechka-87	8.0	.863	(.038)	.823	(.036)
Malyi Kebezh	8.0	.960	(.072)	.933	(.060)
Sobach'ya Rechka	8.0	.846	(.125)	.834	(.105)
Listvyanka	8.0	.912	(.031)	.871	(.036)
Yayl'u	8.0	.855	(.045)	.776	(.043)
Smokotino	7.0	.929	(.033)	.886	(.037)
Mean	7.9	.894	(.057)	.862	(.054)
<i>Pinus cembra</i>					
Ust'-Chornaya	4.0	.686	(.025)	.707	(.045)
<i>Pinus koraiensis</i>					
Malokhekhtsirskoye	6.0	.967	(.062)	.914	(.052)
Khor	7.0	.920	(.037)	.929	(.066)
Sikhote-Alin'	6.0	1.034	(.070)	.964	(.031)
Mean	6.3	.974	(.058)	.936	(.051)

¹Number means year of sampling of material; see text for origins of populations.

(0.686), but we regard this value only as a preliminary one because of the limited sample size and number of loci studied. Nevertheless, it may also be the real level of selfing, probably due to the limited number of trees in the studied locality and a low stand density.

Shaw and others (1981) note that we can conclude the role of inbreeding components other than selfing per se in consanguineous matings (for example, mating between closely related neighbor trees in a population with family structure or assortative/selective pollination/fertilization between genetically similar trees) from the difference between the values of multi- and single-locus estimates. In our study of stone pines these differences, for nearly all samples, appear to be negligible (the difference, in general, does not exceed 0.04). This implies a rather weak effect of mating between relatives or, in other words, absence of microsubdivision of the population.

Furnier and others (1987) found that genetic and physical distances between clumps of *Pinus albicaulis* fail to correlate. The authors related this fact to the effective "mixing" of seeds in the process of their dispersal by the Clark's nutcracker (*Nucifraga columbiana* Engelm). We can expect to observe randomization of such kind (more closely spaced seedlings or clumps are not more related ones) in any other pine species depending on the European nutcracker (*N. caryocatactes* L.) in their dispersal, since the effectiveness of nutcrackers as seed dispersers has been repeatedly proved by numerous investigations (Lanner 1980, 1990; Tomback and Linhart 1991).

Selection Against Inbred Progeny—What may cause "disappearance" of heterozygote deficiency observed among embryos, as compared to adult trees of the population

(figs. 1 and 2)? This can, most likely, be the result of selection against inbred progeny formed by self-pollination, as well as selection in favor of heterozygotes (overdominance). Both selections may increase heterozygosity up to the equilibrium level, but only as a result of negative assortative fertilization or selection in favor of heterozygotes (balancing selection) can heterozygosity also exceed Hardy-Weinberg expectations. This process can be detected with the aid of isozyme gene markers if they are either involved in it directly or are in gametic linkage disequilibrium with selectively significant genes (Crow and Kimura 1970).

In natural conifer populations heterozygosity of adult trees is often higher than in embryos (see Bush and Smouse 1992; Krutovskii and others 1988; Politov and others 1992, for review). For instance, in *Pinus radiata* (Plessas and Strauss 1986) heterozygosity of young trees (17 to 20 years) exceeded that of 5-year seedlings and in the latter it was higher than in embryos. Yazdani and others (1985) found higher heterozygosity of young and adult Scots pine trees as compared to embryos; differences between the young and the adult trees were slight indicating the action of selection exactly at early stages. For stone pines we can suggest a particular life stage of natural selection acting against homozygotes—when groups of seedlings begin to germinate out of nutcrackers' caches competing for resources. It is noteworthy that Eurasian stone pines (as compared to white-bark pine) display multistem forms rarely, which may be the result of intensive competition between seedlings of the same cache.

More direct evidence was obtained in experiments carried out by Farris and Mitton (1984), who studied embryos and seedlings of yellow pine (*Pinus ponderosa*) and found the increase of heterozygosity with age. Muona and others (1987) revealed heterozygosity deficit in Scots pine embryos and its "disappearance" in 1.5-year-old seedlings.

Inbred progeny elimination at early developmental stages in conifers is also supported by some nonallozyme data (see for example, Koski 1973).

CONCLUSIONS

Study of allozyme variability in stone pines has shown the genetic diversity typical to widespread and abundant conifer species with continuous ranges. Differences between stone pines can be explained by both the events of their recent evolutionary history and adaptive significance of the allozyme variation. Heterozygote deficiency among embryos and slight heterozygote excess in mature trees are common features of stone pines, as well as other conifers. A substantial part of self-pollinated progeny is eliminated during ontogenesis by natural selection.

ACKNOWLEDGMENTS

We are greatly thankful to G. R. Furnier, V. N. Vorobjev, N. A. Vorobjeva, L. I. Milyutin, R. T. Gut, and P. Razumov for providing seeds and aid in their sampling, to Yu. S. Belokon' for helpful assistance in the laboratory analysis, to Yu. P. Altukhov for constant support of our study and very useful comments on this manuscript, and to K. Ritland for kindly providing us with the computer program MLT.

We also appreciate H.-R. Gregorius's invaluable comments that helped to substantially improve the manuscript.

REFERENCES

- Adams, W. T.; Strauss, S. H.; Copes, D. L.; Griffin, A. R., eds. 1992. Population genetics of forest trees: Proceedings of the International Symposium on Population Genetics of Forest Trees; 1990 July 31-August 2; Corvallis, OR, U.S.A. Kluwer Academic Publishers. 420 p. (see also New Forests. 1992. 6.)
- Bobrov, E. G. 1978. Forest-forming conifers of the USSR. Moscow: Nauka. 190 p. [In Russian].
- Brown, A. H. D.; Barrett, S. C. H.; Moran, G. F. 1985. Mating system estimation in forest trees: Models, methods and meanings. In: Gregorius, H.-R., ed. Population genetics in forestry. Lecture Notes in Biomathematics. Vol. 60. Berlin-Heidelberg-New York-Tokyo: Springer-Verlag: 32-49.
- Bush, R. M.; Smouse, P. E. 1992. Evidence for the adaptive significance of allozymes in forest trees. New Forests. 6: 179-196.
- Critchfield, W. B.; Little, E. L. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture. 99 p.
- Crow, J. F.; Kimura, M. 1970. An introduction to population genetics theory. New York: Harper and Row.
- Farris, M. A.; Mitton, J. B. 1984. Population density, outcrossing rate and heterozygote superiority in ponderosa pine. Evolution. 38(5): 1151-1154.
- Fineschi, S.; Cannata, F.; Malvolti, M. E.; Hattemer, H. H., eds. 1991. Biochemical markers in the population genetics of forest trees: Proceedings of the Joint Meeting of the Working Parties S2.04-021 Population Genetics and Ecological Genetics and S2.04-05 Biochemical Genetics of the International Union of Forest Research Organizations (IUFRO); October 1988; Porano, Italy. SPB The Hague: Academic Publishing bv. 251 p.
- Furnier, G. F.; Knowles, P.; Aleksiuik, M. A.; Dancik, B. P. 1986. Inheritance and linkage of allozymes in seed tissue of whitebark pine. Canadian Journal of Genetics and Cytology. 28(4): 601-604.
- Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, B. P. 1987. Effect of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution. 41(3): 607-612.
- Goncharenko, G. G.; Padutov, V. E.; Krutovskii, K. V.; Podzharova, Z. S.; Kirgizov, N. Ya.; Politov, D. V. 1988. Level of genetic variability in *Pinus sibirica* in Altai. Doklady Akademii Nauk SSSR. 299(1): 222-225. [In Russian]. [English translation published by Plenum Publishing Corp. in Doklady Biological Sciences; 1988 September: 139-141].
- Hamrick, J. L.; Godt, M. J. 1989. Allozyme diversity in plant species. In: Brown, A. H. D.; Clegg, M. T.; Kahler, A. L.; Weir, B. S., eds. Plant population genetics breeding and genetic resources. Sanderland, MA: Sinauer Associates: 43-63.
- Koski, V. 1973. On self-fertilization, genetic load and subsequent inbreeding in some conifers. Comm. Inst. For. Fenn. 78(10): 1-40.
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P. 1987. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. I. Genetic control of isozyme systems. Genetika. 23(12): 2216-2228. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1988 June: 1568-1576].
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P. 1988. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. II. Level of allozyme variability in Western Sayan. Genetika. 24(1): 118-124. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1988 July: 81-86].
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P.; Milyutin, L. I.; Kuznetsova, G. V.; Iroshnikov, A. I.; Vorob'ev, V. N.; Vorob'eva, N. A. 1989. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. IV. Genetic diversity and differentiation between populations. Genetika. 25(11): 2009-2032. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1990 May: 1343-1362].
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Yu. P. 1990. Interspecific genetic differentiation of Eurasian stone pines for isoenzyme loci. Genetika. 26(4): 694-707. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1990 October: 440-450].
- Krutovskii, K. V.; Politov, D. V. 1992. Study of intra- and interspecific genetic differentiation between Eurasian cedar pines using isozyme loci and multidimensional analysis. In: Symposium on molecular mechanisms of genetic processes: proceedings. Moscow: Nauka Publishers: 87-96. [In Russian].
- Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: 6th North American Forest Biology Workshop: proceedings; 1980 August 11-13. Edmonton, AB: University of Alberta: 15-47.
- Lanner, R. M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.
- Ledig, F. T. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. In: Soulé, M. E., ed. Conservation biology: the science of scarcity and diversity: 77-104.
- Muller-Starck, G.; Ziehe, M., eds. 1991. Genetic variation in European populations of forest trees: proceedings of the workshop on genetic variation in forest tree populations in Europe; 1990; Gottingen, Germany. Frankfurt am Main: Sauerlander's Verlag. 271 p.
- Muona, O.; Yazdani, R.; Rudin, D. 1987. Genetic change between life stages in *Pinus sylvestris*: allozyme variation in seeds and planted seedlings. Silvae Genetica. 36(1): 39-42.
- Plessas, M. E.; Strauss, S. H. 1986. Allozyme differentiation among populations, stands, and cohorts in Monterey Pine. Canadian Journal of Forest Research. 16(6): 1155-1164.
- Podogas, A. V.; Shurkhal, A. V.; Semerikov, V. L.; Rakitskaya, T. A. 1991. Genetic variability of needle tissue enzymes of Siberian cedar pine (*Pinus sibirica* Du Tour). Genetika.

- 27(4): 695-703. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1991 October].
- Politov, D. V. 1989. Allozyme polymorphism, genetic differentiation, and mating system in Siberian stone pine *Pinus sibirica* Du Tour. Moscow: Institute of General Genetics, Russian Academy of Sciences. 190 p. Thesis. [In Russian].
- Politov, D. V.; Krutovskii, K. V.; Altukhov, Yu. P. 1989. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. III. Linkage relationships among isozyme loci. *Genetika*. 25(9): 1606-1618. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1990 March: 1053-1063].
- Politov, D. V.; Krutovskii, K. V. 1990. Genetic variability in Siberian stone pine, *Pinus sibirica* Du Tour. V. Analysis of mating system. *Genetika*. 26(11): 2002-2011. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1991 May: 1309-1316].
- Politov, D. V.; Krutovskii, K. V.; Altukhov, Yu. P. 1992. Isozyme loci characteristics of gene banks of populations of cedar pines. *Genetika*. 28(1): 93-114. [In Russian]. [English translation published by Plenum Publishing Corp. in Soviet Genetics; 1992 July: 76-95].
- Ritland, K. 1990. A series of FORTRAN computer programs for estimating plant mating system. *Journal of Heredity*. 81: 235-237.
- Ritland, K.; El-Kassaby, Y. A. 1985. The nature of inbreeding in a seed orchard of Douglas fir as shown by an efficient multilocus model. *Theoretical and Applied Genetics*. 71: 375-384.
- Ritland, K.; Jain, S. 1981. A model for the estimation of outcrossing rate and gene frequencies using n independent loci. *Heredity*. 47(1): 35-52.
- Shaw, D. V.; Kahler, A. L.; Allard, R. W. 1981. A multilocus estimator of mating system parameters in plant populations. *Proceedings of the National Academy of Sciences (USA)*. 78: 1298-1302.
- Strauss, S. H.; Bosquet, J.; Hipkins, V. D.; Hong, Y.-P. 1992. Biochemical and molecular genetic markers in biosystematic studies of forest trees. *New Forests*. 6: 125-158.
- Szmidt, A. E. 1982. Genetic variation in isolated populations of stone pine (*Pinus cembra*). *Silva Fennica*. 16(2): 196-200.
- Szmidt, A. E.; Muona, O. 1989. Linkage relationships of allozyme loci in *Pinus sylvestris*. *Hereditas*. 111: 91-97.
- Tomback, D. F.; Linhart, Y. B. 1991. The evolution of bird-dispersed pines. *Evolutionary Biology*. 4: 185-219.
- Yazdani, R.; Lindgren, D.; Rudin, D. 1985. Gene dispersion and selfing frequency in a seed-tree stand of *Pinus sylvestris* (L.). In: Gregorius, H. R., ed. *Population genetics in forestry. Lecture Notes in Biomathematics*. Vol. 60. Berlin-Heidelberg-New York-Tokyo: Springer-Verlag: 139-154.

GENETIC POPULATION STRUCTURE AND GROWTH FORM DISTRIBUTION IN BIRD-DISPERSED PINES

Diana F. Tomback
William S. F. Schuster

Abstract—At least nine species of the 20 wingless-seed pines are dependent on the nutcrackers (*Nucifraga*) for seed dispersal. Seed dispersal by nutcrackers influences several aspects of population structure: (1) tree dispersion patterns and growth form distribution, (2) genetic relationships among trees within populations, and (3) genetic diversity among populations. Studies to date of three species, whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*), and Swiss stone pine (*Pinus cembra*), provide examples of intrapopulation genetic relationships and growth form distribution; other recent work provides some information for interpopulation comparisons.

Of the 20 species of pines with large, wingless seeds (collectively considered "stone pines"), nine are known dependents on the nutcrackers, *Nucifraga* (Corvidae), for seed dispersal (Tomback and Linhart 1990 and references therein). Five of these bird-pines are in the Subsection *Cembrae*, two in *Strobi*, and two in *Parrya*; for classification see Critchfield and Little (1966). For several species of these bird-dependent pines, other corvids, squirrels, or other rodents may also make varying contributions to tree establishment (see, for example, Hayashida 1989; Ligon 1978; Vander Wall 1992), but the factor in common to all dispersers is the tendency to remove seeds from the vicinity of parent trees and "scatterhoard" them (bury small clusters of seeds in subterranean caches for future use). Clark's nutcrackers (*N. columbiana*) bury one to 15 or more seeds per cache at distances of several meters to 22 km from parent trees (Hutchins and Lanner 1982; Tomback 1978, 1982; Vander Wall and Balda 1977). Eurasian nutcrackers (*N. caryocatactes*) bury up to 24 seeds per cache and travel similar distances (see, for example, Bibikov 1948; Mattes 1982; Mezheny 1961; Turcek 1966).

Thus, nutcrackers create a highly unpredictable seed shadow, with seedling establishment often occurring several kilometers from parent trees (Tomback and others 1990). Nutcracker-dispersed seeds may end up in small, isolated areas, particularly following disturbances such as fires. In large, open or disturbed areas, different nutcrackers may cache seeds from several different stands

of parent trees, resulting in a haphazard distribution of seeds with respect to seed source (Tomback 1978, 1982). Also, nutcrackers often bury more than one seed per cache (mean of three or four seeds per cache for Clark's nutcracker, Tomback and Linhart 1990), and the seeds may come from the same parent tree (Tomback 1988; Tomback and Knowles 1989).

In contrast, most wind-dispersed seeds fall within about 120 m of parent trees and are dependent on prevailing winds for dispersal (see, for example, McCaughey and others 1986). Updrafts and wind patterns associated with storms may send wind-dependent seeds over longer distances and in other directions, and seed-storing rodents may move seeds around locally (Vander Wall 1992). However, because the seeds of these species usually move relatively short distances and establishment is often in small, disturbed patches, a family structure (local aggregations of related genotypes) frequently results within populations (see, for example, Knowles 1984; Linhart 1989; Linhart and others 1981; see also Furnier and others 1987; Tomback and Linhart 1990).

These different seed-dispersal modes, bird vs. wind, may lead to different genetic population structures. Genetic population structure results from nonrandom spatial distribution of genotypes (Epperson 1990, and references therein). Plant populations may show structure on different scales, such as among populations and within populations. The common methods for investigating genetic population structure are based on allozyme analysis, comparing populations or subpopulations by means of either allele frequencies, Wright's F_{ST} or Nei's G_{ST} statistics, or spatial autocorrelation.

Seed dispersal by nutcrackers influences several levels of population structure in wingless-seed pines. Within populations, it affects both (1) tree dispersion patterns (whether individuals are clumped vs. spaced) and, consequently, growth form distribution and (2) genetic relationships among trees. Among populations it affects genetic diversity. In this paper, we explore the specific impacts of nutcracker seed-dispersal behavior on each of these aspects of population structure.

GROWTH FORM DISTRIBUTION

Research to date on three species of bird-dispersed pines—whitebark pine (*Pinus albicaulis*) (Furnier and others 1987; Linhart and Tomback 1985), limber pine (*P. flexilis*) (Carsey and Tomback 1992; Linhart and Tomback 1985; Schuster and Mitton 1991), and Swiss stone pine (*P. cembra*) (Tomback and others 1993)—

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Diana F. Tomback is Associate Professor of Ecology, Department of Biology and Center for Environmental Sciences, University of Colorado at Denver, Denver, CO, 80217-3364. William S. F. Schuster is Forest Director, Black Rock Forest Consortium, Box 483, Cornwall, NY 12518.

indicates that trees within populations occur in three different growth forms. The single-trunk growth form is typical of conifers and consists of a single genet (individual). Also composed of a single genet, the multi-trunk growth form has two or more trunks either contiguous at the base or fused at the base or part way up the bole. Multi-trunk trees may be the consequence of a tendency toward side-branching and lack of apical dominance, particularly under stressful environmental conditions, such as unstable soils, aridity, or mechanical damage to the leader (Schuster and Mitton 1991; Weaver and Jacobs 1990). Although the tree cluster growth form is also composed of two or more contiguous or fused trunks, the trunks consist of different genets (individuals). This growth form results from the germination and survival of more than one seedling from a seed cache (growth form terminology from Tomback and others 1990).

The latter two growth forms have similar morphologies and thus cannot be distinguished with certainty without genetic analysis (Schuster and Mitton 1991; Tomback and others 1993) (figs. 1, 2). Consequently, in field surveys of frequency distribution of different growth forms, we combined the multi-trunk and tree cluster forms together in



Figure 2—Swiss stone pine (*Pinus cembra*) multi-trunk tree. Protein electrophoresis indicated that both trunks had the same genotype.

the category “tree clumps” (term from Lanner 1980; the same as “multi-trunk trees of unknown origin,” Tomback and others 1990). For reporting the results of field surveys of tree clump frequency in populations, we use the term “tree site” to refer to the small area of ground supporting either a single-trunk tree, a multi-trunk tree, or a tree cluster.

Overall, tree clumps accounted for 19 to 90 percent of the tree sites surveyed in three species of bird-dispersed pines (whitebark, limber, and Swiss stone) (table 1). Whitebark pine in the two stands surveyed had the highest percentage of tree sites occupied by clumps. In the two studies of limber pine combined, the percentage of tree sites with clumps ranged from 24 to 48; the latter population occurred on a steep, southeast-facing slope with gravelly soil at 3,310 m elevation. Carsey and Tomback (1992) also examined 17 tree sites in a stand of krummholz limber pine above timberline (3,460 m elevation) and found clumps at all tree sites. For Swiss stone pine, clumps were found at 19 to 30 percent of the tree sites and up to 45 percent of seedling sites. In the Piz da Staz study area, the highest percentage of Swiss stone pine clumps occurred at higher elevations, but this did not hold for the Muottas Muragl study area.



Figure 1—Swiss stone pine (*Pinus cembra*) tree cluster. Protein electrophoresis indicated that each trunk is a different genet.

Table 1—Percentage of tree clumps (combined multi-trunk trees and tree clusters) in surveyed populations of three species of bird-dispersed pines

Species and location	Elevation	Tree sites	Maximum trunks per clump	Percent sites with clumps	References
	<i>Meters</i>				
Swiss stone pine					
Switzerland	1,835	406	6	21	Tomback and others 1993
	2,070	351	6	30	
	1,835	96	4	29	
	2,125	43	5	19	
Whitebark pine					
California	2,850	50	5+	90	Tomback and Linhart 1990
Montana	2,730	50	5+	58	
Limber pine					
Colorado	1,650	361	7	30	Schuster and Mitton 1991
Colorado	2,585	105	3	35	Carsey and Tomback 1992
	2,810	135	4	24	
	3,310	140	4	48	

The preferred laboratory method for distinguishing tree clusters from multi-trunk trees has been starch gel protein electrophoresis to assay the genotype of seed (Furnier and others 1987) or foliage tissue obtained from each trunk of a tree clump (Carsey and Tomback 1992; Linhart and Tomback 1985; Schuster and Mitton 1991; Tomback and others 1993; for review of technique, see Kephart 1990). Those clumps that have two or more trunks with different genotypes are classified as tree clusters. Unfortunately, this technique may underestimate slightly the numbers of tree clusters, because seeds within nutcracker caches tend to be genetic relatives and thus may inherit similar genotypes (Carsey and Tomback 1992; Schuster and Mitton 1991). In a few cases tree cluster members may possess identical genotypes at the gene loci examined, so the clusters are misclassified as multi-trunk (single-genotype) trees. The procedures for calculating the probability of such errors are presented in Schuster and Mitton (1991).

For studies of whitebark pine, limber pine, and Swiss stone pine combined, genetic analysis indicated that 18 to 100 percent of the tree clumps sampled were tree clusters (table 2). The low value, 18 percent, was obtained by Schuster and Mitton (1991) for a limber pine population in the Pawnee National Grasslands, at the periphery of the range of both the pine and Clark's nutcracker. The high values of 100 percent for limber pine and 83 percent for whitebark pine were based on small sample sizes (n = six clumps in both cases, Linhart and Tomback 1985). Furnier and others (1987) found that 58 and 70 percent, respectively, of the whitebark pine clumps they sampled in two stands contained more than one genotype; they did not sample all trunks of some clumps, so these percentages are conservative. Clumps in four limber pine stands were studied by Carsey and Tomback (1992), with percentages of clusters ranging from 24 percent above timberline to 81 percent at 2,810 m elevation. Of the Swiss

stone pine clumps sampled in one stand, 70 percent were tree clusters (Tomback and others 1993). Remarkably, an examination of the number of gene loci used for each study in table 2 shows no relationship with the percentage of clusters determined for each sample (Spearman rank correlation, $r_s = -0.406$, $n = 12$, NS). With the exception of the limber pine clumps analyzed by Schuster and Mitton (1991), which represented all the clumps in the population, the clumps examined in the studies in table 2

Table 2—Percentage of tree clumps (combined multi-trunk trees and tree clusters) found to be tree clusters (growth form with more than one genet) in three species of bird-dispersed pines

Species	Clumps examined	Gene loci used	Percent clusters	References
Swiss stone pine	23	4	70	Tomback and others 1993
Whitebark pine	6	4	83	Linhart and Tomback 1985
	12	11	58	Furnier and others 1987
	23	11	70	
Limber pine	7	2	57	Linhart and Tomback 1985
	6	4	83	
	6	4	100	
	108	10	18	Schuster and Mitton 1991
	18	7-9	56	Carsey and Tomback 1992
	21	7-9	81	
	18	7-9	44	
	17	7-9	24	

represented a sample of the total number of clumps present and were sometimes not selected entirely at random. For the studies by Furnier and others (1987) and Carsey and Tomback (1992), only reproductively mature tree clumps were sampled; for the studies by Linhart and Tomback (1985) and Tomback and others (1993), clumps were usually sampled as encountered, but an effort was made to include some seedlings and young trees.

Only three studies permit an estimate of the overall percentage occurrence of tree clusters among tree sites in populations (table 3). Limber pine tree clusters in the Pawnee National Grasslands population occurred at only 5 percent of the total tree sites. For limber pine in the Front Range, clusters occurred at similar percentages of tree sites, 19 to 21, despite differences in elevation. Clusters of Swiss stone pine occupied 21 percent of the tree sites in the upper subalpine population.

Apparently, tree clusters typically occupy a substantial proportion of the tree sites in each population of whitebark, limber, and Swiss stone pine. Moreover, the percentage of individual genets in a population that are found in clusters is much higher than the proportion of tree sites supporting clusters. Based on the previous studies, 12 to 40 percent of the individuals in populations of bird-dispersed pines occur in a highly clumped spatial pattern, primarily as a consequence of seed dispersal by nutcrackers.

If stress plays a role in the growth of the multi-trunk form from a single genet, as proposed by Schuster and Mitton (1991) and Weaver and Jacobs (1990), then we might predict a relatively higher percentage of multi-trunk trees in more stressful environments. In fact, about 25 percent of the limber pine tree sites in the Pawnee National Grasslands population support multi-trunk trees (from tables 1 and 2). This area is at lower elevations (1,650 m) on the plains east of the Rocky Mountains, at the eastern boundary of the limber pine range, and trees may be subjected to stress factors such as grazing, fire, unstable slopes, heat, and extreme aridity (Lepper 1974; McNaughton 1984; Schuster and Mitton 1991). The highest estimated percentages of multi-trunk limber pine trees in the Front Range populations studied by Carsey and Tomback (1992) occurred in the upper subalpine population (27 percent, elevation 3,310 m) and in the population above timberline (76 percent, elevation 3,460 m), where winds and accompanying desiccation are extreme and the

Table 4—Estimated mean and standard error of relatedness of individuals within and between limber pine tree clusters

Mean	Standard error	References
Within tree clusters		
0.19	0.10	Schuster and Mitton 1991
.43	.13	Carsey and Tomback 1992
Between tree clusters		
.01	.04	Carsey and Tomback 1992

soil is gravelly and unstable. We also calculated that only 9 percent of the tree sites of the upper subalpine population of Swiss stone pine supported multi-trunk trees. In contrast to the former study areas, the Swiss stone pine tree sites are not typically characterized by aridity and poor soils, which may explain the relatively low frequency of multi-trunk trees (Tomback 1988).

We should note here that tree clusters are not known to occur in Colorado pinyon pine (*Pinus edulis*), which is dispersed by both Clark's nutcrackers and pinyon jays (*Gymnorhinus cyanocephalus*). Vander Wall and Balda (1977) report that only one seed from each cache grows to maturity.

GENETIC RELATIONSHIPS

Relationships Within and Between Tree

Clusters—Because nutcrackers tend to harvest and pouch several seeds from the same pine cone and visit more than one cone from the same tree or genet (if a cluster) (Tomback 1988; Tomback and Knowles 1989), they tend to place sibling seeds in the same seed cache. During a bumper whitebark pine cone crop (1989) in Yellowstone National Park, Tomback and Knowles (1989) observed nutcrackers taking entire pouchloads of 28 to 97 seeds ($\bar{x} = 53$ seeds, $n = 8$) from a single cone or individual tree (genet) or trunk.

One consequence of this behavior is the tendency for individuals in tree clusters to be genetic relatives—either half-siblings, siblings, or the products of selfing. Furnier and others (1987) found that individuals within tree clusters of two populations were genetically more similar (smaller genetic distance) than individuals in different tree clusters. Individuals within clusters differed by a mean of 1.66 alleles; individuals of different clusters differed by a mean of 5.82 alleles or greater (of 11 gene loci). Two studies examined genetic relatedness within limber pine clusters using the Quellar and Goodnight (1989) estimator (table 4): For tree clusters in the Pawnee National Grasslands population, Schuster and Mitton (1991) determined that individuals were related on average as half-siblings. In addition, they determined that cluster members that had fused together at the base were more closely related on average ($r = 0.35$) than cluster members that had not fused ($r = 0.05$). Carsey and Tomback (1992) calculated that cluster members in their upper subalpine population (3,310 m elevation) were related on average as between half and full siblings; members of different clusters were unrelated on average (table 4).

Table 3—Estimated percentage of tree sites that support clusters of individuals in populations of two species of bird-dispersed pines

Species	Percent clusters	Elevation	References
<i>Meters</i>			
Swiss stone pine	21	2,050 to 2,240	Tomback and others 1993
Limber pine	5	1,650	Schuster and Mitton 1991
	19	2,585	Carsey and Tomback 1992
	19	2,810	
	21	3,310	

Possible Biological Implications of Tree

Clustering—Despite the fact that tree clusters occur commonly in populations of bird-dispersed pines and include a large proportion of the genets in the population, little is known of the biology of this growth form (Tomback and others 1993). Several papers have speculated about the potential advantages and disadvantages to individuals growing in clusters (Schuster and Mitton 1991; Tomback and Linhart 1990; Tomback and others 1993).

Individuals in clusters may have higher survivorship than single genets under certain environmental conditions because of morphological or physiological benefits (Bullock 1981; Keeley 1988; Mattes 1982). A sturdy, well-anchored structure might better resist the strong winds and mechanical damage of higher elevation environments. Root grafting may also occur among cluster members, particularly relatives (Schuster and Mitton 1991), resulting in efficient water and nutrient acquisition (Holtmeier 1986). In addition, since nutcrackers may establish pines at some distance from conspecifics, for example, in burned areas or disturbed patches, individuals in tree clusters may cross-pollinate and thus avoid selfing (Tomback and Linhart 1990). This might produce a high proportion of sound seeds, particularly if clusters consisted of both relatives and nonrelatives. Finally, both Schuster and Mitton (1991) and Tomback and Linhart (1990) point out that the occurrence of kin groups of bird-dispersed pines may result in kin selection as an evolutionary force. Possible consequences for cluster members may include some decrease in competition or facilitation of rootgrafting.

With respect to the potential disadvantages to individuals growing in clusters, one area of possible fitness loss is reproductive output. For limber pine trees in three stands in the Colorado Front Range (same populations studied by Carsey and Tomback 1992), cluster members produced fewer male and female cones than did single-trunk trees during each of 3 years (Feldman 1991; Feldman and Tomback 1991). Reduction of reproductive output may result from competition among cluster members for moisture, nutrients, and space. These effects may be exacerbated for limber pine, which typically grows on windy, xeric sites with poor soils in the Colorado Front Range (Feldman 1991; Feldman and Tomback 1991). Feldman (1991) and Feldman and Tomback (1991) noted that trees in clusters had smaller diameters than did similarly aged single-trunk trees, supporting the possibility of competition.

Another possible disadvantage to cluster members is that their seeds may be more inbred than seeds produced by single-genet trees, because of pollen exchange within clusters (Furnier and others 1987; Tomback and Linhart 1990). Politov and Krutovskii (1990) provide some evidence for this in Siberian stone pine (*Pinus sibirica*), which is dispersed by the Eurasian nutcracker. Examining the mating system of Siberian stone pine in seven populations, they noted an excess of homozygotes among seed embryos in the majority of their samples. They attributed this to a relatively high rate of self-pollination, but pollination among related cluster members would have a similar effect.

Genetic Spatial Structure Within Populations—

Several studies indicate that in many wind-dispersed conifers there is family structure within populations (local aggregations of genetic relatives) (see, for example, Knowles 1984; Linhart 1989; Linhart and others 1981). This is the consequence of seed dispersal typically restricted to short distances (Furnier and others 1987; Tomback and Linhart 1990), and the availability of local, disturbed patches for colonization (see, for example, Linhart and others 1981). In contrast, Furnier and others (1987) did not find any evidence of family structure among the neighboring tree clusters in two whitebark pine populations (although cluster members tended to be related). They attributed this lack of family structure with respect to geographic distance to the seed-caching behavior of Clark's nutcrackers. Since Clark's nutcrackers do not defend caching territories, several different nutcrackers may cache in one area, often bringing seeds in from different stands of trees (Tomback 1978, 1982). This probably results in a haphazard distribution of related seed caches (Furnier and others 1987; Tomback and Linhart 1990). The Eurasian nutcracker in Sweden (Swanberg 1956) and in the Alps (Mattes 1982) stores many of its caches within territories defended by pairs. However, the seeds cached in these territories are both from local and more distant parent trees (up to 15 km, Mattes 1982), so there is also considerable mixing in any area. Politov and Krutovskii (1990) examined seven populations of Siberian stone pine and also found no evidence for intrapopulation substructure.

GENETIC DIVERSITY

Generally speaking, conifers show less genetic diversity among populations (mean $G_{ST} = 0.068$) than do other kinds of plants (mean $G_{ST} = 0.250$) (Hamrick and Godt 1990). After an extensive review of the plant literature, Hamrick and Godt (1990) concluded that animal-dispersed species have more differentiated populations (higher G_{ST} values) than do wind-dispersed species. But, seed dispersal by nutcrackers, which occurs routinely over large distances, might actually result in higher levels of gene flow than from seed dispersal by wind and thus lower levels of population differentiation.

Few studies have examined interpopulation variation in bird-dispersed pines. Schuster and others (1989) genetically analyzed two limber pine populations at extreme ends of a 1,700-m elevational transect in the Colorado Front Range. They determined that pollen flow along this gradient was impeded by pollination phenology; populations separated by more than 400 m elevation did not have overlapping pollination periods. For the populations at each end of the transect, allele frequencies differed significantly at eight of the 10 loci studied. However, the calculated number of migrants exchanged between the populations per generation ($N_m = 11.1$) was well above the level required to overcome genetic drift. Given the very different environmental conditions of the two populations, Schuster and others (1989) concluded that natural selection rather than lack of gene flow may have differentiated the populations. They also suggested that seed dispersal

by Clark's nutcrackers is likely to be "a more important component of gene flow in limber pine than pollen transfer, at least across elevational gradients."

Schuster and Mitton (1992) also compared five populations of limber pine across a 100-km range and found low levels of differentiation (mean $G_{ST} = 0.035$). Hamrick (unpublished data cited in Betancourt and others 1991) examined eight populations of pinyon pine (*Pinus edulis*) and found a slightly greater differentiation (mean $G_{ST} = 0.077$).

Nine populations of the Siberian stone pine were studied by Krutovskii and others (1989) to examine interpopulation genetic differentiation. Their results indicated only slight differences among populations. Using Nei's measures of diversity, they determined that on average about 98 percent of allozyme variation was attributed to intrapopulation variability and only 2 percent to interpopulation variability (mean $G_{ST} = 0.022$). However, they did find a significant correlation between geographical distance and genetic differences among populations, but only for populations separated by 400 km or more. They also found a higher level of differentiation among populations within the same region than between regions, which may reflect adaptation to local environmental conditions. The high level of intrapopulation variation in Siberian stone pine is very similar to what has been found for most wind-dispersed conifer species (Krutovskii and others 1989).

EVOLUTIONARY IMPLICATIONS

Tomback and Linhart (1990) speculated that bird-dispersed pines might be more prone to genetic drift than are wind-dispersed species. The ranges of these pines, particularly subalpine species, tend to be highly fragmented, and small, isolated populations are not uncommon. These smaller populations may show founder effects, particularly loss of rare alleles. In addition, because of the occurrence of tree clusters and the potential for cross-pollination among cluster members, there may be high rates of inbreeding in these populations. When effective population size is smaller than 100, genetic drift can be far more potent in causing gene frequency changes than natural selection (Futuyma 1986 and references therein). It is possible that the evolution of cone, seed, and tree morphology in bird-dispersed pines was in part the consequence of new traits that arose from a combination of drift and inbreeding in small, isolated populations. Nutcrackers, or ancestral corvids, selected for preferred traits and spread these traits to other populations or founded new populations with these traits.

If bird-dispersed pines have this population structure, Tomback and Linhart (1990) make two predictions: "(1) there is greater genetic variation among populations of bird-dispersed pines than among wind-dispersed pines, and (2) there are small, isolated populations of bird-dispersed pines with highly differentiated gene pools compared to one another and, particularly, compared to large populations that may regularly experience some gene flow from other large populations."

Although the earliest populations of bird-dispersed pines may have had the characteristics described by Tomback

and Linhart (1990), the findings of Krutovskii and others (1989), Schuster and Mitton (1992), and Hamrick (unpublished data cited in Betancourt and others 1991) do not support the first prediction, and it may well be that the great distances over which nutcrackers disseminate seeds provide effective gene flow. Betancourt and others (1991) describe a disjunct population of Colorado pinyon pine in northern Colorado that was the result of a founding event probably about 400 years ago. Compared to other pinyon pine populations, the average percentage of polymorphic loci and number of alleles per locus were reduced, although levels of heterozygosity were not affected. These, however, are typical founder effects (Betancourt and others 1991; Futuyma 1986). Within the last century, the founding population has given rise to four descendant populations, three with fewer than 50 trees each (Premoli and others 1993). The two smallest, most distant descendant populations had fewer alleles per polymorphic locus and reductions in individual heterozygosity compared to the larger populations. The mean G_{ST} value of 0.060 indicated little differentiation among populations. Because tree clusters do not occur often in Colorado pinyon pine, these new populations may not adequately test prediction 2. However, they do demonstrate that seed dispersal by birds results in small, isolated founding populations. Much more work is required to thoroughly characterize the genetic population structure of bird-dispersed pines and to address questions concerning the biology of tree clusters.

ACKNOWLEDGMENTS

We thank Konstantin Krutovskii and Dmitri Politov for providing translations of their papers and for interesting discussions during the workshop. In addition, we are grateful to Jeff Karron, Andrea Premoli, and Kathleen Shea for helpful comments on an earlier draft of the paper. Support for DFT for attending the SSPE Workshop was provided by the College of Liberal Arts and Sciences, University of Colorado at Denver.

REFERENCES

- Betancourt, J. L.; Schuster, W. S.; Mitton, J. B.; Anderson, R. S. 1991. Fossil and genetic history of a pinyon pine (*Pinus edulis*) isolate. *Ecology*. 72(5): 1685-1697.
- Bibikov, D. I. 1948. On the ecology of the nutcracker. *Trudy Pechorskogo-Ilychskogo Gosudarstvennogo Zapovednika*. 4(2): 89-112. [In Russian, translated by L. Kelso].
- Bullock, S. J. 1981. Aggregations of *Prunus ilicifolia* (Rosaceae) during dispersal and its effect on survival and growth. *Madroño*. 28: 94-95.
- Carsey, K. S.; Tomback, D. F. 1992. Growth form distribution and genetic relationships in tree clusters of *Pinus flexilis*, a bird-dispersed pine. Manuscript.
- Critchfield, W. F.; Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.

- Epperson, B. K. 1990. Spatial patterns of genetic variation within plant populations. In: Brown, A. H. D.; Clegg, M. T.; Kahler, A. L.; Weir, B. S., eds. *Plant population genetics, breeding, and genetic resources*. Sunderland, MA: Sinauer Associates: 229-253.
- Feldman, R. 1991. Growth form and reproductive output in limber pine: the cost of mutualism. Denver, CO: University of Colorado at Denver, Department of Biology. 46 p. Thesis.
- Feldman, R.; Tomback, D. F. 1991. Growth form and reproductive output in limber pine: the cost of mutualism. Manuscript.
- Furnier, G. R.; Knowles, P.; Clyde, M. A.; Dancik, B. P. 1987. Effects of avian seed dispersal on the genetic population structure of whitebark pine populations. *Evolution*. 4(3): 607-612.
- Futuyma, D. J. 1986. *Evolutionary biology*. 2d ed. Sunderland, MA: Sinauer Associates. 600 p.
- Hamrick, J. L.; Godt, M. J. W. 1990. Allozyme diversity in plant species. In: Brown, A. H. D.; Clegg, M. T.; Kahler, A. L.; Weir, B. S., eds. *Plant population genetics, breeding, and genetic resources*. Sunderland, MA: Sinauer Associates: 43-63.
- Hayashida, M. 1989. Seed dispersal by red squirrels and subsequent establishment of Korean pine. *Forest Ecology and Management*. 28: 115-129.
- Holtmeier, F. -K. 1986. Über Bauminseln (Kollektive) an der klimatischen Waldgrenze—unter besonderer Berücksichtigung von Beobachtungen in verschiedenen Hochgebirgen Nord-amerikas. *Wetter und Leben*. 38: 121-139.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Keeley, J. E. 1988. Population variation in root grafting and a hypothesis. *Oikos*. 52(3): 364-366.
- Kephart, S. R. 1990. Starch gel electrophoresis of plant isozymes: a comparative analysis of techniques. *American Journal of Botany*. 77(5): 693-712.
- Knowles, P. 1984. Genetic variability among and within closely spaced populations of lodgepole pine. *Canadian Journal of Genetics and Cytology*. 26: 177-184.
- Krutovskii, K. V.; Politov, D. V.; Altukhov, Y. P.; Milyutin, L. I.; Kuznetsova, G. V.; Iroshnikov, A. I.; Vorob'ev, V. N.; Vorob'eva, N. A. 1989. Genetic variability in the Siberian stone pine, *Pinus sibirica* Du Tour. IV. Genetic diversity and the extent of genetic differentiation between populations. *Genetika*. 25(11): 2009-2032. [Translation published by Plenum Publishing Corp. in 1991].
- Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Dancik, B. P.; Higginbotham, K. O., eds. *Sixth North American forest biology workshop: proceedings*. Edmonton, AB: University of Alberta: 15-48.
- Lepper, M. G. 1974. *Pinus flexilis* James and its environmental relationships. Davis, CA: University of California at Davis, Graduate Group in Ecology. 197 p. Dissertation.
- Ligon, J. D. 1978. Reproductive interdependence of piñon jays and piñon pines. *Ecological Monographs*. 48: 111-126.
- Linhart, Y. B. 1989. Interactions between genetic and ecological patchiness in forest trees and their dependent species. In: Bock, J. E.; Linhart, Y. B., eds. *Evolutionary ecology of plants*. Boulder, CO: Westview Press: 1-31.
- Linhart, Y. B.; Mitton, J. B.; Sturgeon, K. B.; Davis, M. L. 1981. Genetic variation in space and time in a population of ponderosa pine. *Heredity*. 46: 407-426.
- Linhart, Y. B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. *Oecologia*. 67: 107-110.
- Mattes, H. 1982. Die Lebengemeinschaft von Tannenhäher und Arve. *Berichte Eidenössische Anstalt für das forstliche Versuchswesen, Birmensdorf*. Nr. 241. 74 p.
- McCaughy, W. W.; Schmidt, W. C.; Shearer, R. C. 1986. Seed-dispersal characteristics of conifers in the Inland Mountain West. In: Shearer, R. C., comp. *Proceedings—conifer tree seed in the Inland Mountain West symposium; 1985 August 5-6; Missoula, MT*. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 50-62.
- McNaughton, G. M. 1984. Comparative water relations of *Pinus flexilis* at high and low elevations in the central Rocky Mountains. Laramie, WY: University of Wyoming, Department of Botany. 59 p. Thesis.
- Mezhenny, A. A. 1961. Food competitors, enemies and diseases. In: Egorov, O. V., ed. *Ecology and economics of the Yakut squirrel*. Moscow: Akademiya Nauk: 124-129.
- Politov, D. V.; Krutovskii, K. V. 1990. Genetic variation of Siberian stone pine *Pinus sibirica* Du Tour. V. Analysis of mating system. *Genetika*. 26(11): 2002-2011. [Translation published by Plenum Publishing Corp. in 1991].
- Premoli, A. C.; Chischilly, S.; Mitton, J. B. 1993. Levels of genetic variation captured by four descendant populations of pinyon pine (*Pinus edulis* Engelm.). Manuscript.
- Quellar, D. C.; Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution*. 43: 258-275.
- Schuster, W. S. F.; Alles, D. L.; Mitton, J. B. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational transect. *American Journal of Botany*. 76(9): 1395-1403.
- Schuster, W. S. F.; Mitton, J. B. 1991. Relatedness within clusters of a bird-dispersed pine and the potential for kin interactions. *Heredity*. 67: 41-48.
- Schuster, W. S. F.; Mitton, J. B. 1992. Gene flow in limber pine. II. Data for five populations. Manuscript in preparation.
- Swanberg, P. O. 1956. Territory in the thick-billed nutcracker *Nucifraga caryocatactes*. *Ibis*. 98: 412-419.
- Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. *The Living Bird*. 16: 123-161.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology*. 51: 451-467.
- Tomback, D. F. 1988. Nutcracker-pine mutualisms: multi-trunk trees and seed size. In: Ouellet, H., ed. *Acta XIX Congressus Internationalis Ornithologici*, Vol. 1; 1986 June 22-29. Ottawa, ON: University of Ottawa Press: 518-527.

- Tomback, D. F. 1988. [Unpublished observations in the Upper Engadine Valley of Switzerland, October 1988].
- Tomback, D. F.; Knowles, J. W. 1989. Post-fire whitebark pine seed dispersal by Clark's nutcracker in Yellowstone National Park. Unpublished data and observations.
- Tomback, D. F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology*. 4: 185-219.
- Tomback, D. F.; Hoffmann, L. A.; Sund, S. K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-129.
- Tomback, D. F.; Holtmeier, F. -K.; Mattes, H.; Carsey, K. S.; Powell, M. L. 1993. Tree clusters and growth form distribution in *Pinus cembra*, a bird-dispersed pine. *Arctic and Alpine Research*. [In press].
- Turcek, F. J. 1966. Über das Wiederauffinden von im Boden versteckten Samen durch Tannen-und Eichelhäher. *Waldhygiene*. 6: 215-217.
- Vander Wall, S. B. 1992. The role of animals in dispersing a "wind-dispersed" pine. *Ecology*. 73: 614-621.
- Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs*. 47: 89-111.
- Weaver, T.; Jacobs, J. 1990. Occurrence of multiple stems in whitebark pine. In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 156-159.

Basic Ecology



International Workshop
St. Moritz 1992

EXPERIENCES WITH REPRODUCTION OF CEMBRA PINE

Ernst Frehner
Walter Schönenberger

Abstract—As regards reproduction, cembra pine (*Pinus cembra* L.) is a special case. If the greater part of the seeds are stolen by nutcrackers, they should be harvested before they are ripe and then matured. With correct treatment it is possible to store seeds for up to 7 years. After soaking in water, germination began almost at once. The separate steps along the long process from harvesting via seed extraction, maturation, storage, testing, sowing, and transplantation to planting out are described in detail.

This study reports our experiences over many years of seed and afforestation trials with cembra pine (*Pinus cembra* L.), from seed harvesting to planting.

Cembra pine is a special case as regards reproduction (Frehner and Fuerst 1992). The extreme conditions in its natural environment at the upper timberline strongly influence flowering, fertilization, and seed maturation, so that the quantity and quality of seed varies from year to year (table 1). The results of repeated studies on cone quality, maturation, and storage vary correspondingly.

The special features of reproduction in cembra pine begin with seed collection. Except in full mast years, most of the seeds have been eaten or collected by the nutcracker by the time of their natural maturation. Like the seeds of many other tree and shrub species, those of cembra pine require several months of dormancy. Maturation of the seed and time of extraction is therefore very important for the development of the embryo. To better exploit full mast years, the durability of the seeds should be extended through improved storage methods. It is also important that stored seeds should be induced to germinate and produce successful saplings at short notice. Also in terms of sowing, transplantation, and potting, cembra pine requires special conditions.

SYMBIOSIS WITH THE NUTCRACKER

The importance of the nutcracker for the natural distribution of cembra pine is undisputed. The detailed study by Mattes (1982) on this relationship concludes that without the nutcracker there would be no cembra pine forests

in the Alps, and that the existing stands would diminish considerably within a few generations.

Depending on the number of cones produced, the nutcracker stores seeds as winter provisions in numerous caches, usually numbering over 10,000, each containing from three to five seeds, but only consumes about 80 percent of its reserve. The remaining seeds contribute greatly to the regeneration of cembra pine stands. The nutcracker may transport seeds over a distance of 15 km or more and over a difference in height of up to 600 m.

CONE COLLECTION

In years with normal, moderate fructification, the nutcracker begins to pick the seeds at medium altitudes as soon as ripening has begun, about mid-August, and continues to do so until about the end of September. This means that collecting cones is a race with the bird. If cones are to be collected in years with partial mast, this must be done at an early stage, while they are still unripe, before the birds begin their robbery, and then stored under optimum conditions for maturation.

In long-term observations, 19 percent of the years produced full mast, 55 percent partial mast, and 26 percent failed to produce (Mattes 1982). As a rule it is only in full mast years that enough seeds ripen on the tree to make harvesting worthwhile; in this case the nutcracker does not have time to devour or carry away all the remaining seeds.

Neither color nor size of cones has any influence on seed quality or planting success. The costs of harvesting and seed extraction are considerably greater for small cones.

With early harvesting it is very important that the seeds should be allowed to ripen under optimum conditions of moisture and warmth, as the embryos are in a very early stage of development (only up to 3 mm long).

Studies on protected cones attached to mother trees at 2,000 m have shown that the length of the embryo hardly changes between mid-September and the end of October. In contrast, embryos in cones harvested early (mid-September) have elongated by 3-4 mm. This shows that

Table 1—Characteristics of cembra pine seed crops

Harvesting time per tree	about 1 hour
Yield per tree	about 15 kg cones
Number of cones per tree	about 150-200
Weight per cone	60-100 g
Seed yield (fresh weight)	20-30 percent
Number of living seeds per cone	50-70
Thousand-seed weight	300-400 g

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Ernst Frehner is former Head of the Research Nursery, Walter Schönenberger is Head of the Research Section Silviculture, Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland.

Table 2—Cone collection, maturation, and seed extraction

September	Cone harvesting (embryo length up to 3 mm)
September	Stratification of cones for maturation at 10-20 °C for 8-10 weeks
November	Seed extraction (embryo length 3-5 mm)

it is not worthwhile enclosing whole trees in nets or treating the cones with chemicals. Early harvesting and favorable conditions of stratification are preferable to late harvesting.

CONE MATURATION

Stratification (storing cones in layers in a moist, airy substrate) is the simplest and most certain technique of accelerating ripening and reducing inhibition of germination so that the seeds are ready to germinate quickly. Stratification simulates the natural conditions of moisture and warmth prevailing in the forest, or may even be better.

The freshly harvested cones are stored in layers at a proportion of one part cones to five parts substrate. Suitable substrates are washed sand or a mixture of sand and peat. The substrate must be sieved so that its particles are smaller than the seeds. The stratified cones should then be stored in a cupboardlike container with good drainage that protects the cones from attack by mice or birds.

The development of the embryos depends greatly on the temperature of the substrate and the water content of the cones. Studies have shown that the embryos develop only slowly at low temperatures, while high temperatures also have a negative influence. The best results were obtained with substrate temperatures alternating between 10 and 20 °C. It is advisable to keep the stratified cones in a protected place (for example, an unheated plastic tunnel or glasshouse), where the temperature may rise toward 25 °C during the day and sink to about 5 °C at night. Naturally, the temperature within the substrate does not vary so greatly.

Moisture is very important. The substrate should be moist and airy, and the cones should be just moist enough to prevent the seed coat from shrinking away from the endosperm. Maturation to the point of seed extraction proceeds much better under moist conditions than with dry storage. With ripening under dry conditions the germination rate is 50 percent lower than that after moist storage, while dormancy is 10 times longer.

SEED EXTRACTION

After 8 to 10 weeks' stratification, the seeds can be extracted. The cones, which are by this time beginning to disintegrate, are sieved out of the substrate, left to dry for a while, and then rubbed through finer sieves to separate the seeds from scales and cone axes. The finer scales and substrate particles can then be removed through further

sieving and washing in a water bath, either immediately or after another ripening process. In a water bath the unfertilized seeds (empty seed cases) float to the top and can be decanted. To summarize, the course of cone maturation is shown in table 2.

SEED MATURATION

The treatment of the seeds after extraction depends on their intended use and how long they are to be stored.

Under natural conditions it takes 2 to 3 years for the seeds to germinate after the cones have fallen. This may be due to many factors, for example, hard and impermeable seed cases, incomplete development of the embryo, or inhibiting substances in the endosperm, in the seed case, or elsewhere in the seed. In cembran pine, the main reason is the low stage of development of the embryos: at the time of harvesting the embryos are not more than 3 mm long.

With artificial maturation using variable temperatures, the period between harvesting and germination can be reduced to one winter. Here, the aim is to induce the embryos to grow from a length of 3 mm or less to the germination length of 7-9 mm (table 3). To promote embryo growth even after seed extraction, the seeds are alternately exposed to warmth and cold in a monthly rotation. Exposure to warmth for periods of more than 4 to 6 weeks does not positively influence embryo development. Great attention should be paid to water content throughout the whole period of seed treatment, as during cone storage. The better the seed maturation, the better the embryo development and, consequently, the better the seeds are suited for drying and storage.

BASIC PRINCIPLES OF STORAGE

After drying, the seeds are placed in one of the container types mentioned and stored under cool conditions. In the early stages they should be regularly inspected.

Water content:

- the lower the water content, the lower the storage temperature;
- the lower the storage temperature, the longer the seeds can be stored;
- the longer the seeds have been stored, the longer they must be stratified before sowing.

Table 3—Results of the maturation of cembran pine seeds (harvested September 22) after warm-cold-warm treatment

Features	September 23	February 28
Seed length (peeled)	9.5 mm	10.4 mm
Channel length	4.5 mm	8.5 mm
Embryo length	1.0 mm	8.4 mm
Seeds with visible embryos	11 percent	72 percent
Seeds ready to germinate	96 percent	76 percent

Storage containers:

- at high water content (>20 percent), in perforated plastic bags;
- at low water content (<15 percent), in airtight containers accommodating 2-5 kg.

Storage rooms: climatized:

- for short-term storage with high water content, 1-3 °C;
- for fairly long storage with low water content, -5 to -10 °C.

Freeze drying has proved unsuitable for cembran pine seeds, because the water content is too high.

Fungal attack: for prevention, the seeds should be treated with a fungicide and regularly examined as to smell and condensed moisture indicating a too-high water content in the containers; if this occurs, the seeds should be dried immediately.

STORAGE OF MATURE SEEDS

Without treatment for reduction of water content the seeds cannot be stored longer than one winter. With reduction of water content to about 25 percent, the seeds can be stored at 1-3 °C for up to 3 years without great loss in the germination rate.

Later trials showed that gently handled seeds could be dried to a water content of 15 percent, and that under storage at -5 to -10 °C the germination capacity did not decrease for up to 7 years. A water content of more than 20 percent rendered storage below 0 °C unfeasible.

THREE SEED TREATMENTS

After seed extraction three treatments for three different storage periods can be defined as:

- Treatment 1: for immediate sowing without storage (table 4).
- Treatment 2: for storage over 2 to 3 years (table 5).
- Treatment 3: for storage over 3 to 7 years (table 6).

GERMINATION TRIALS

Germination trials begin in December. The seeds are sown in a sterile peat/sand in sterilized containers, being

Table 4—Treatment 1: for immediate sowing without storage

November	Seed stratification outdoors for 5-6 months; substrate three parts washed sand to one part seeds
April	Sowing (usually 30-50 percent of seeds lie-over)
Advantages:	No need for climatization
Disadvantages:	No storage possible, annual seed harvesting necessary, high proportion of lie-over, high risk of robbery by birds and mice

Table 5—Treatment 2: for storage over 2-3 years with high water content under refrigeration in plastic bags (for example, in years with partial or full mast)

November	Seed stratification for 4-6 weeks at 16-18 °C in washed sand
December/January	Sieving and cleaning of seeds; drying of seeds for 1-2 weeks at 16-18 °C to about 25 percent water content; embryo length increases to 5-7 mm
January	Storage of seeds in perforated plastic bags at 1-3 °C over 2-3 years
October	Seeds are soaked for 1-2 days; stratification outdoors for 6 months in washed sand
April/May	Sowing (no lie-over to be expected)
Advantages:	Allows storage for up to 3 years without lie-over
Disadvantages:	Storage climatized at 1-3 °C necessary, high water content, risk of rotting and fungal infection, long stratification period

normally spread and pressed down, then covered with about 1 cm sand or substrate. The trials are best conducted in rooms without direct sunlight; the ideal temperature is 16 to 18 °C. Alternating temperatures have a positive effect. The seeds should be watered by hand according to need. Storage in greenhouses with automatic spraying has not proved suitable. The germination tests take 6-8 weeks.

Table 6—Treatment 3: for storage in airtight containers for 3-7 years with low water content and freezing temperatures (for example, for seeds harvested in good partial or full mast years)

December	Seed stratification; first warm treatment at 16-18 °C for 4-5 weeks
January	Cold treatment at 1-3 °C for 4-5 weeks
February	Second warm treatment at 16-18 °C for 4-5 weeks until germination begins; embryo length increases to 7-9 mm
February	Sieving and cleaning of seeds; drying at 16-18 °C for 1-2 weeks to 15 percent water content
March	Storage in airtight plastic bags or glass containers at -5 to -10 °C for 3-7 years
April	Defrosting for 1-2 days, soaking in lukewarm water for 1-2 days, sowing
Advantages:	Seeds can be stored for up to 7 years, no lie-over, short-term stratification (6-8 weeks), good mast years and seed quality can be fully exploited
Disadvantages:	Long-term deep-freezing required

SOWING

The seeds are sown between the end of April and mid-May. The number of seeds to be sown depends on the results of the germination trials. Because germination is slow, the seeds should be sown in boxes resistant to mice and birds. The best substrates are soils without limestone mixed, according to conditions and pH, with peat (which loosens the soil, maintains a pH between 5 and 6, and regulates the moisture level) or raw humus containing mycorrhizal fungi from cembran pine stands. The seed and transplantation beds should continuously be occupied by cembran pines except for short periods with green fertilizing.

Cembran pine grows best in thickly sown beds, with 1,200 to 1,800 seedlings per square meter, grown for 2 to 3 years in a seedbed.

If the seeds begin to germinate during stratification, they should be sown immediately. If this is unfeasible, they can be frozen at -3 to -4 °C and sown as required. Seeds that have already germinated and whose radicle is longer than 1 cm should not be planted in a seedbed, but thinned out; otherwise the resulting plants are liable to be worthless, with tortuous root collars, short stems, small crowns, and few fine roots. Size, quality, and yield are definitely better in thinned seedlings. Shortening the roots causes deformations.

We did not run any trials with sowing in autumn, as the risks of attack by mice and birds and also snow pressure on the protection lattice are then very high.

TRANSPLANTING

The specially designed beds are continuously supplemented with acid soil (for example, peat) and if necessary with chalk-free acid fertilizer. To hinder invasion by weeds and frost heaving and to restrict evaporation, and

also to maintain a good soil structure, the beds are mulched.

It is recommended that 3-year-old saplings be transplanted in spring or summer (from mid-July). This can be done by machine, with a spacing of 10 by 18 cm. Saplings with poor root development should be discarded, as it is not worth planting them out. The saplings stay in the transplanting bed for 3 years.

POTTING

High-altitude afforestations are exposed to high risks from extreme weather conditions, snow, and pests. Experience has shown that seedlings in peat-fiber pots succeed better than those with naked roots, especially on difficult sites, so potting is recommended. The production of potted plants has been described by Schönenberger and others (1990). It is important to keep the pots well watered. The saplings should only be planted out when the root tips begin to penetrate through the peat-fiber pots.

REFERENCES

- Frehner, Ernst; Fürst, Ernst. 1992. Vom Samen bis zur Pflanze. Ein Erfahrungsbericht aus dem Forstgarten. Ber. Eidgenöss. Forsch. anst. Wald Schnee Landsch. 333. 47 p.
- Mattes, Hermann. 1982. Die Lebensgemeinschaft von Tannenhäher und Arve. Eidg. Anst. forstl. Versuchswes., Ber. 241, 74 S.
- Schönenberger, Walter; Frey, Werner; Leuenberger, Franz. 1990. Ökologie und Technik der Aufforstung im Gebirge - Anregungen für die Praxis. Eidg. Anst. forstl. Versuchswes., Ber. 325, 58 S.

Translation: Margaret Sieber

DISTRIBUTION AND ECOLOGY OF SIBERIAN STONE PINE IN THE URALS

P. L. Gorchakovsky

Abstract—The northern and southern boundaries of the distribution area of Siberian stone pine (*Pinus sibirica*) in the Urals and in the adjacent plains are examined; the main sociological factors limiting boundary positions are described. There is a natural tendency of this species to spread northward and southward, from places recently invaded, but this process is usually stopped or turned back by human influence. Numerous occurrences of Siberian stone pine beyond its present continuous range indicate that the former distribution area of this species was larger in the past than at present.

Siberian stone pine (*Pinus sibirica*), or briefly Siberian pine, is considered to be one of the most valuable species of coniferous trees growing in Russia. Research on the limits of natural distribution of Siberian pine, on their causes and dynamics, is of indisputable theoretical and practical interest. Research is especially necessary for scientific substantiation of rational use of all forests, particularly those with Siberian pine, for the definition of measures to protect it from being exterminated, and for solving the problems concerning possible cultivation of this species in adjacent regions.

The general distribution area of Siberian pine includes: (1) northeastern regions of the European part of Russia (the farthest west locality is in the upper reaches of the Vychegda River); (2) the Ural Mountain range; (3) western Siberia; (4) middle and eastern Siberia (up to the Aldan River); and (5) mountain ranges of Altai, the Transbaikalian area, and northern Mongolia.

The main limiting factors of the distribution of this species are: heat deficiency in the north; permafrost, peatland, and severe winter in the northeast; water deficiency and low air humidity in the south.

The western part of the area is located in the Ural Mountains and in the northeastern regions of the European part of Russia adjacent to them. Siberian pine occupies rather large areas within the territory of Sverdlovsk and Perm provinces, Komi Republic, and within Knanty-Mansy national district of Tyumen province.

THE NORTHERN LIMIT

The northern border of the distribution area (fig. 1) passes along the Izhma-Pechora watershed, advances

considerably northward (up to 65°30' N. latitude) along the valley of the Pechora River and even farther northward (67° N. latitude—the northern polar circle). Then it switches back south in the form of a tongue, to the foothills of the elevated eastern part of the Russian plain. From Telpos-Iz Mountain, 64° N. latitude, it leaps northward along the eastern slope of the Polar and Prepolar Urals reaching 66°10' N. latitude. It then recedes southward in the space between the rivers, but returns northward again in a tongue-shaped projection along the valley of the Ob River.

Besides that, a few isolated occurrences of Siberian pine are known outside its main distribution area.

The northern limit of Siberian pine does not reach the extreme boundaries of the distribution of larch (*Larix sibirica*) and spruce (*Picea obovata*). The well-known Russian botanist B. N. Gorodkov (1929) supposed that the advancement of Siberian pine to the north is restricted because its seeds do not get ripe under the severe conditions of the short growing season.

However, the latest observations demonstrate that even at the northern limit of the distribution area seeds of Siberian pine usually get ripe. The main reason likely is that Siberian pine is not able to develop its root system under low soil temperature (Tyrtikov 1954). In cold soils, the roots of Siberian pine ramificate comparatively weakly and grow more slowly than the roots of spruce and larch. Consequently, insufficient soil heating during the growing season impedes normal development of root systems, and this appears to be the main factor limiting the distribution of Siberian pine in the north. Under the severe climatic conditions of northern Siberia, pine does not grow on cold, peatland soils.

Close to the northern boundaries, in the upper reaches of the Pechora River, Siberian pine selects the warmest well-heated locations, inhabiting even the riverside limestone outcrops and cliffs. Contrary to that, in the regions farther south, for example in the middle and southern Urals, Siberian pine never grows in such habitats because the riverside limestone cliffs are too warm during daylight periods.

In the plains adjacent to the Urals (the Pechora and western Siberian lowlands), the far-north occurrences of Siberian pine are restricted to the valleys of the large rivers (the Pechora, the Ob, and some of their tributaries). The boundary deviates northward in the form of narrow strips along the river valleys. In marshy areas between the rivers, however, where superficial bedding of permafrost frequently occurs, the border line is farther south. Under plain conditions, the river valleys characteristically have more permeable ground, lower levels of permafrost bedding, and warmer soils that are more favorable to

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

P. L. Gorchakovsky is Professor, Doctor of Biology, Chief Scientist at the Institute of Plant and Animal Ecology, Russian Academy of Sciences, Ural Branch, 620219, Ekaterinburg, Russia.

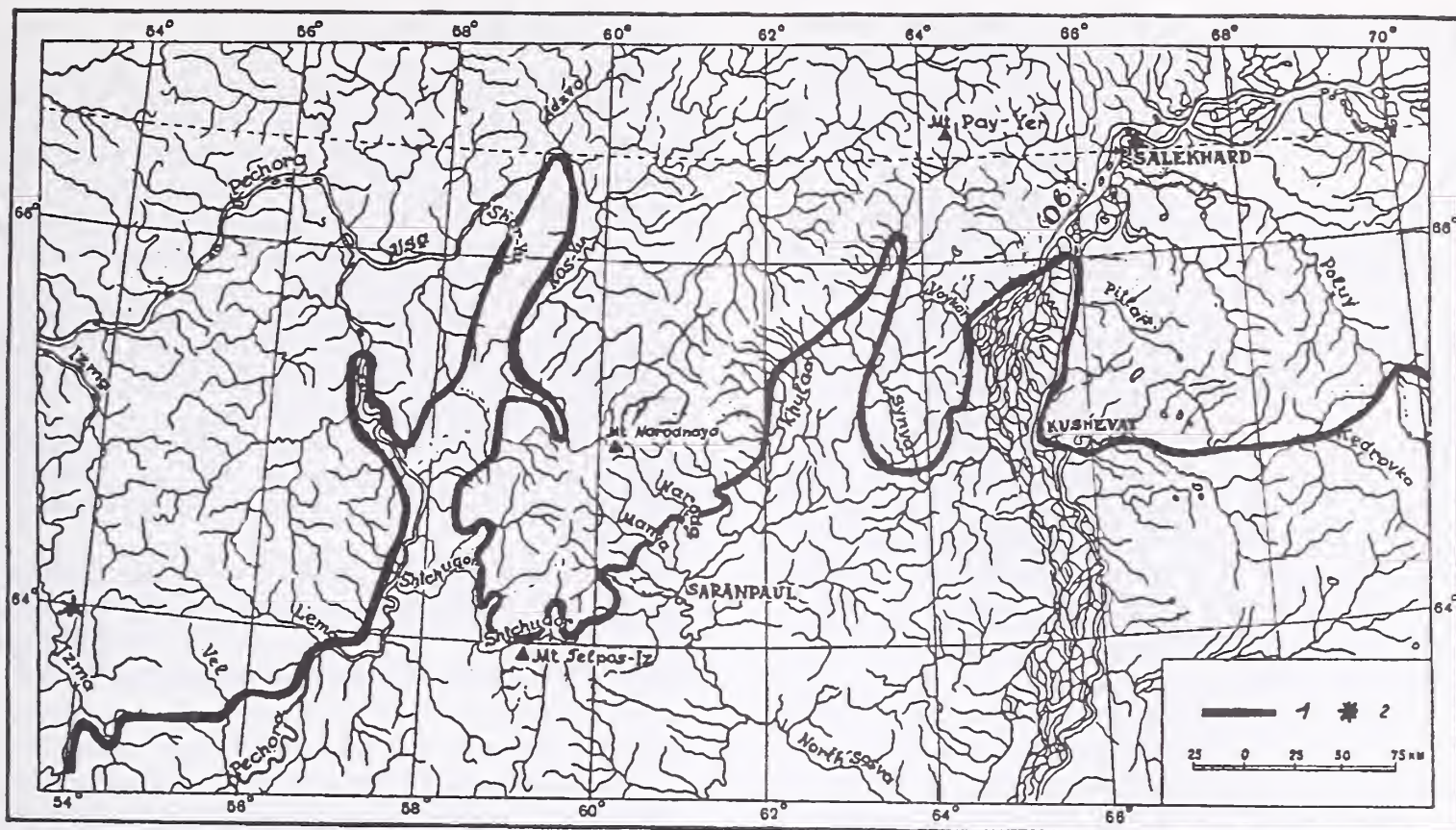


Figure 1—Northern distribution limit of Siberian stone pine in the Urals and in the adjacent plains. * = isolated occurrences.

Siberian pine. Moreover, one should bear in mind that the valleys of the large rivers that bring masses of comparatively warm water from the south are characterized by a warmer local climate favorable to the growth of Siberian pine.

At the Lyapin depression, in the region of Saranpaul, Siberian pine-dominated forests are to be found on buried palsa peatbogs covered by sandy loam deposits. On hill-ocks, better conditions for drainage and heating of the superficial layer of accumulated deposits favor the formation of rather tall Siberian pine forests. On the other hand, raised bogs with pools and ridges between the hillocks are treeless. The level of permafrost here is rather high; ice-lenses are found inside the peaty hillocks.

In the plains, at the extreme limit of its distribution area, Siberian pine is usually represented by solitary specimens dispersed within spruce-larch-birch forests; trees usually are healthy, without signs of atrophy; their trunks reach 10 to 14 m in height.

Within the western and eastern outskirts of the Ural Mountain range, the Siberian pine border displaces northward along meridionally oriented low foothills and mountain ridges. There, this species grows on slopes or near brooks and small rivulets under moderate or slightly increased (flowing) ground moisture conditions. The advance northward is promoted by a variety of sites suitable for forest growth as well as by favorable drainage, better soil heating, and consequently by lower depth of permafrost.

In the watershed of the Urals there are huge mountains topped by woodless tundralike "goltsy" summits, located

within the mountain tundra and high-mountain cold desert belts (Gorchakovsky 1975, 1989). They are characterized by a more severe climate, and consequently the northern limit of Siberian pine is considerably displaced southward.

Siberian pine almost absolutely escapes the mountain massif of the Prepolar Urals from the west; its distribution is restricted to the Pechora lowland; in rare cases it occurs in the mountain part along deep erosion-tectonic valleys of the large rivers.

On the eastern slope of the Prepolar Urals, however, Siberian pine ascends rather high in the mountains, almost to the upper forest limit. In the "subgoltsy" belt (analogous to the subalpine belt), in the region of Gorodkov Mountain (Sale-Ur-Oika), Siberian pine shows dwarfed growth (2.5 to 5 m in height), exhibiting trunks thickened at the basal portion of the tree and tapering upward, and with wide-branched crowns of low stability. Frequently, such dwarfed trees bear abundant cones. At lower elevations, within the mountain-taiga belt in the plain, Siberian pine reaches 10 m in height. From the eastern side, along the foothills, this plant extends to the Polar Urals reaching 66°10' N. latitude in the mountains of the so-called Small Urals.

More intensive advancement of Siberian pine northward, along the eastern slope of the Ural Mountain range, was favored partly by historical causes. This species invaded from Siberia to new places in the Urals. It arrived earlier on the eastern slope of the Ural Mountain range, favored mainly by the specific natural conditions of the eastern slope. The eastern slope of the Prepolar and

Polar Urals has a more continental climate than the western slope. Relative air humidity is lower here; annual precipitation including that in the winter is less heavy; and snow cover melts earlier in spring. Consequently, the growing season is longer, and the top soil layer is better heated.

On its northern boundaries, Siberian pine is distributed disjunctively and occurs as dispersed small clumps or solitary specimens in the taiga. All these extreme localities are rather disjunct from each other. This may be explained primarily by the fact that only in rare locations are the combinations of various environmental factors favorable for growth of Siberian pine at the limits of its range. On the other hand, the dispersion of this species has been reduced here and there due to forest fires, extension of bogs, trampling of seedlings and young growth by reindeer, and extermination by humans. In locations where human activity is reduced to a minimum, Siberian pine invades new places north of its present limit. This advance is observed especially clearly in the mountain regions of the Urals.

THE SOUTHERN LIMIT

The southern borderline of continuous distribution of Siberian pine (fig. 2) passes through the Russian plain near the city of Perm; then it turns southward along the western slope of the middle Urals, reaching the most southern position at 56°10' N. latitude; then it switches back north following the eastern slope of the middle Urals until retiring into western Siberia.

A few outliers occur beyond this limit. The most interesting of them are to be found in the mountain dark coniferous taiga of the southern Urals in the region of the town of Zlatoust and in the Ilmen Mountains.

At the southern limit of its range, Siberian pine usually grows in the form of single-standing, tall trees. Only on rocky outcrops does it exhibit prostrated growth forms (krummholz).

Natural regeneration of Siberian pine near the southern boundary of its distribution is generally satisfactory. However, there are many factors unfavorable to regeneration, such as seed collection difficulties, fires, and trampling of

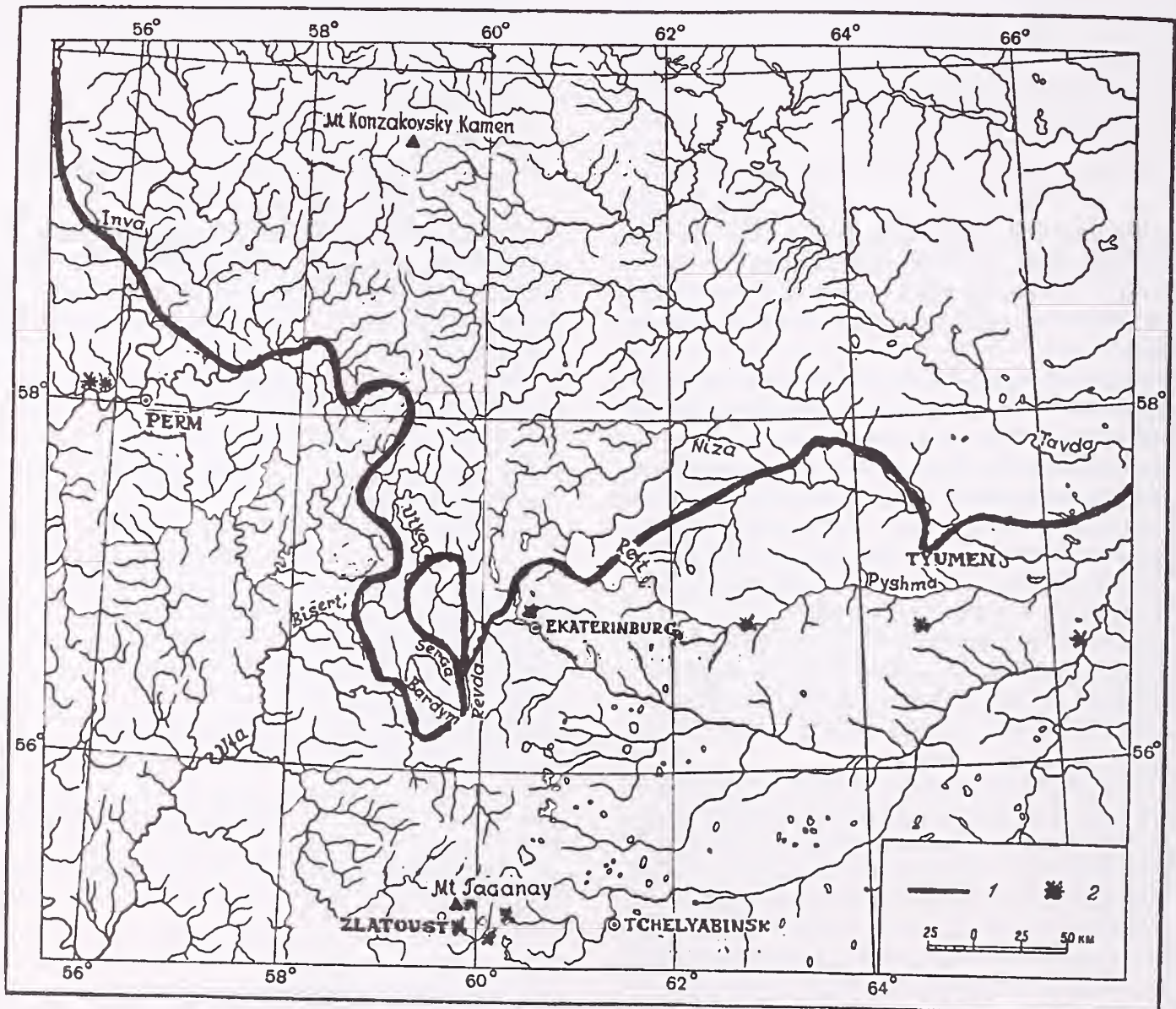


Figure 2—Southern distribution limit of Siberian stone pine in the Urals and in the adjacent plains. * = isolated occurrences.

seedlings by livestock. In locations where such unfavorable influences are absent, or they manifest themselves to a lesser degree, regeneration of Siberian pine is usually good. So, for example, Siberian pine reproduces very successfully on raised sites protected from fire within the Bakhmet Bog, which is surrounded by Scots pine forests in the basin of the Pyshma River.

Along the western slope of the Urals, as well as in certain sites within the watershed zone where the climate is more humid, Siberian pine has invaded new places significantly farther south than in the Preural and Transural regions. Its southern limit projects southward in the form of tongues that comprise the western slope and part of the watersheds of the mountain range. Climate of the eastern slope of the middle Urals is drier; the amount of precipitation is less compared to the western slope. Therefore, on the eastern slope of the mountain range and in the foothills zone adjacent to it (the region of predominance of Scots pine forests), Siberian pine occurs considerably farther north.

Within the peatland between the rivers of the western Siberian plain, the southern limit of Siberian pine turns south again. There Siberian pine grows mainly on raised sites within bogs, where it is well protected from fire.

Siberian pine invaded the southern Urals later than spruce and fir (*Abies sibirica*) and has not had enough time in the prehistoric period to reach the climatically influenced limit of its distribution. Human activities hampered the southward advance of Siberian pine into new places along the Ural Mountain range. Here and there, numbers of this species have declined. Several centuries ago Siberian pine had been distributed farther south in the Urals compared to its contemporary limit. Since then it has receded northward due to forest fires and human impact. There is clear evidence of recent decline in total distribution. In the southern part of the area, Siberian pine occurs sporadically in small groves, groups of trees, or as single trees. It grows in places least endangered by fire, most frequently on moist soils in the headwater regions and valleys of brooks and rivulets, on the margins of bogs and on raised sites within them, on lake shores (somewhere close to water), and on steep outcrops of acid rocks.

Formerly, the region of continuous distribution of Siberian pine extended south at least to the isolated localities mentioned earlier, but probably this tree species extended even farther south. Literature data as well as oral statements by local residents provide evidence of it. Siberian pine disappeared from these places not only due to cutting of timber and forest fires, but also because local inhabitants picked all the cones, often before cones were completely ripe. They also dug up seedlings for transplanting into personal gardens.

DISCUSSION AND CONCLUSIONS

The rather complicated picture of distribution of Siberian pine in the Urals depends to a large extent on climatic differences between the relatively humid western slope of the range and the more continental eastern slope.

Humidity of the western slope restricted the northward advance of Siberian pine, but favored its advance to the south. On the contrary, continentality of the eastern slope favored the advance of this species northward, but restricted its advance southward.

At both the northern and southern limits of its distribution, Siberian pine does not occur high up in the mountains. Its northernmost occurrences in high mountains are in the eastern part of the Prepolar Urals.

In the northern Urals, Siberian pine is widespread almost everywhere in the high-mountain belts. On certain mountains (Oika-Nyor, Pas-Nyor, Chistop, and others), however, it forms the upper forest limit. High-mountain Siberian pine-dominated forests grow on steep slopes with poorly developed soils. Near the upper forest limit, such forests may be found mainly in less high mountains far removed from large mountain massives. In such isolated mountains, the upper forest limit is caused chiefly by edaphic factors, while the climate of their treeless zone and of the subgoltsy belt is less severe. Dwarfed, prostrate, and, in most cases, noncone-producing specimens of Siberian pine of the northern Urals occur in high-mountain tundras significantly higher in elevation than the normal upper forest limit. For instance, dwarf specimens occur on the mountains Isherim, Oika-Chahl, Yalping-Nyor, Denezhkin Kamen, Konzhakovsky Kamen, Kosvinsky Kamen, and others. The occurrences of krummholz growth forms above the normal upper forest limit have to be explained by the dispersal of seeds into the mountain tundra zone by the nutcracker and rodents.

In the middle Urals near the summits of relatively high mountains, Siberian pine also forms singly standing, dwarfed trees (the mountains Kachkanar, Starick-Kamen, and others). South of Mount Starick-Kamen, this species is never found in high-mountain belts, but in the forest belt its area spreads considerably farther south.

Judging by its biological and ecological features, Siberian pine may not be considered as a species becoming extinct. It is perfectly well adapted to the taiga environment; it is a good cone producer, and, if human impact does not interfere, it regenerates quite satisfactorily. Almost everywhere, regeneration occurs close to old trees. However, one should bear in mind that Siberian pine grows more slowly than other shade-tolerant coniferous trees. Therefore, ground fires that annihilate second-growth trees adversely affect natural regeneration of this species.

The border lines of Siberian pine, especially on the southern border, have been reduced by careless and sometimes barbarian treatment of this valuable plant. It is necessary to secure proper protective measures for its southern localities in the Urals and to use seeds gathered from trees mainly for sowing under the forest canopy and in tree nurseries.

In the course of intensive harvest cuttings in the dark coniferous fir-spruce forests that have individual Siberian pine trees in the admixture, foresters usually retain Siberian pine as seed trees for natural regeneration. However, in many cases, this does not work well because in the heavy clay and loamy soils of the plains, and in the

mountains on poorly developed soils, such trees run the danger of windfall. To avoid windfall, it is necessary to retain clumps of Siberian pine with accompanying tree species instead of single specimens of Siberian pine.

Natural conditions of the middle Urals and of the mountain-range portion of the southern Urals (at least up to 54° N. latitude) are favorable for regeneration and growth of Siberian pine. This valuable tree species may be reintroduced to areas south of its present distribution. This can be concluded from the successful cultivation of Siberian pine south of its present border line in the mountain taiga regions of the middle and southern Urals.

REFERENCES

- Gorchakovsky, P. L. 1975. The plant world of the high-mountain Urals. Moscow: "Nauka" Publishing. 284 p. [In Russian].
- Gorchakovsky, P. L. 1989. Horizontal and altitudinal differentiation of the vegetational cover of the Ural Mountains. *Pirineos*, N 133: 33-54.
- Gorodkov, B. N. 1929. The Polar Urals in the upper reaches of the rivers Voykar, Synya and Lyapin. In: *Materials of the Committee for Expeditional Researches*, v. 7, Leningrad: 1-28. [In Russian].
- Tyrtikov, A. P. Growth of tree roots at the northern limit of forests. *Bull. of Moscow Soc. of Naturalists. Section of Biology*. 59(1): 72-82. [In Russian].

ECOPHYSIOLOGICAL INVESTIGATIONS ON CEMBRAN PINE AT TIMBERLINE IN THE ALPS, AN OVERVIEW

Rudolf Häsler

Abstract—During the nineteenth century foresters as well as scientists became interested in learning more about cembran pine (*Pinus cembra*) in the Alps, but extensive ecophysiological fieldwork did not begin before the 1930's. Great progress was made after the establishment of permanent field stations at the timberline at Obergurgl (1953), Patscherkofel near Innsbruck (1963), and Stillberg near Davos (1959). In a brief overview, some selected results of ecophysiological research in cembran pine are presented.

The old and bizarre cembran pines (*Pinus cembra* L.), which form the timberline over a wide range in the Central Alps, have always fascinated humans. In earlier days, the tree was of some importance. It produced not only wood but also nuts that could be used as food. Therefore, this tree has been of some interest for a long time, and a lot of books and papers about cembran pine in the Alps have been published, in forestry as well as in biological science.

This short overview presents only some selected examples of the ecophysiological research, with a special focus on gas exchange. A general overview on ecophysiological problems at the timberline was published by Tranquillini (1979). Many other subjects, such as growth, genetics, and mycorrhiza, have been investigated in Austria, France, Italy, and Switzerland but are not mentioned in this overview.

BEGINNING OF INVESTIGATIONS

In the middle of the nineteenth century, foresters became interested in the cembran pines growing in the Alps. Fankhauser (1853) described the distribution of these trees together with the climatological conditions they need for growing well. He mentioned that it is not possible to transfer this tree species to low elevations. Kerner (1866) and Simony (1870) published similar data for parts of Austria. At the same time, the diseases and the insect enemies of the cembran pine in the Alps attained some importance. They have been described by Keller (1890) and others.

ECOLOGICAL AND GEOGRAPHICAL OBSERVATIONS

More and more scientists became interested in cembran pine at the end of the nineteenth century and the early twentieth century to learn more about these trees, which grow on the most extreme sites in the mountains. Monographs concerning cembran pine in Switzerland (Rikli 1909) and in Austria (Nevole 1914) were published. Many other publications were written at this time. The main subjects were growth, and again fungal diseases and problems with insects (Fankhauser 1903; Keller 1901, 1910; and others).

FIRST ECOPHYSIOLOGICAL FIELD EXPERIMENTS

Ecophysiological investigation in the field began in the thirties on Patscherkofel near Innsbruck (Austria). To work near the timberline in the Alps was a logistic problem. The cembran pines only grow near the timberline, at high altitudes. It was extremely hard to work there in earlier times.

Cartellieri (1935) was probably the first to measure photosynthesis and water relations throughout a whole season in cembran pine at timberline. At the same time he also took measurements of different dwarf shrubs at high elevation. He measured photosynthesis by absorbing the carbon dioxide in barite-water, and then he determined the CO₂ assimilation by titration in the laboratory. Some idea about the difficulties of working at the timberline in those days is given in his papers: missing data in the annual course are explained as "walking back to the laboratory I lost some of the probes because some of the glass flasks were broken," or in another example, "at this time I got ill and had to stop the investigation." Nevertheless his results show more or less the same values as we are measuring today with our modern climatized and very expensive instrumentation. Also about the same time Ulmer (1937) investigated the annual course of frost hardiness and measured in parallel the osmotic values in the needles.

PERMANENT FIELD STATIONS AND CONTINUOUS CO₂ MEASUREMENTS

Great progress in timberline research in the Alps was made in the 1950's. Again in Austria, a permanent experimental field station at an altitude of about 1,950 m above sea level (a.s.l.) was established in 1953 near

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Rudolf Häsler is Head of the Section "Forest and Climate," Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland.

Obergurgl. At the same time, the newly developed infrared gas analyzer (IRGA) made it possible to measure continuously carbon dioxide in the air.

Tranquillini (1955) conducted experiments at the new field station at Obergurgl to investigate the relations between light, temperature, and photosynthesis in needles of young cembran pines growing in the sun or in the shadows. He determined the light compensation points for these needles as 500 and 150 Lux, respectively, and the light saturation points as 25 and 18 kLux, respectively. The CO_2 assimilation values he reported reached 2.5 mg and 2.1 mg CO_2/g dry weight, respectively. Net photosynthesis starts at -5°C and has an optimum range between 10 and 15°C . The upper temperature limit is at 35°C .

The microclimatic conditions during wintertime and needle and soil temperatures as well as gas exchange and water relations in young cembran pines growing on natural sites at the timberline were published by Tranquillini (1957). He showed that in wintertime, even in warmer weather conditions, no net photosynthesis was detectable. Holzer (1958) explained this lack of photosynthesis by a changed cell structure as well as by a changed physiological behavior during wintertime.

Pisek and Winkler (1958) measured the annual course of the capacity of net photosynthesis and of respiration in detached shoots of cembran pines growing at different altitudes. During wintertime, they found an always negative carbon dioxide balance in the trees at the timberline, whereas those growing at lower elevations could produce a positive one, at least during periods with temperatures above the freezing point. Keller (1970) confirmed these findings, using another method. Tranquillini (1958, 1963d) investigated the annual course of frost resistance. He found that young trees are more sensitive to frost than mature trees. Young trees become damaged by temperatures between -15 to -30°C , while mature trees can survive temperatures lower than -45°C . Keller and Beda-puta (1973) analyzed stem respiration in cembran pine during wintertime.

Pisek and Winkler (1959) studied photosynthesis in relation to temperature in different light conditions as well as at different altitudes. With increasing light intensity, the temperature optimum is shifted to higher temperatures. There are some difficulties in comparing all these older results with the measurements of today, because not all parameters can be transformed (for example, illumination [Lux]). Some other values, such as the needle surfaces, were normally not used as a reference for gas exchange measurements before the 1980's.

A CO_2 budget for a whole year was estimated by Tranquillini (1959a, 1959b, 1963a, 1963b). Total CO_2 uptake per year (gross photosynthesis) of a 5- to 8-year-old tree at 2,000 m a.s.l. was about 7.8 kg. About 38 percent was lost by respiration from needles, branches, stem, and roots. According to the measured net CO_2 assimilation, a tree should produce 2.2 g dry matter per gram of needles. In reality they produced 0.65 g. The author mentioned that most of the missing carbon dioxide may have been used by the mycorrhiza.

In the second half of the 1950's, ecological investigations with the aim of finding methods for successful

afforestation at high altitude were started in Switzerland (Stillberg, Davos: 2,000-2,230 m a.s.l.) and in Austria (Haggen, Sellraintal: 1,730-1,900 m a.s.l.). Cembran pine was one of the species used in these field experiments, which still are going on. It takes a long time to get results from trees growing at high elevation near the timberline. Summaries containing preliminary results were published by Schönenberger and Frey (1988) for Stillberg and by Kronfuss (1980, 1983, 1986) for Haggen.

LABORATORY CLIMATE CONTROL

The technical possibilities developed fast. On Patscherkofel (1,950 m a.s.l.) a climate laboratory was established in 1963. In this laboratory a device was installed that allows analysis of the gas exchange of young trees in climatized windchannels at high altitude. Now it became possible to control exactly the climatic parameters such as temperature and air and soil humidity as well as windspeed, which was a brand-new innovation. Using this new instrumentation old measurements could be verified and a lot of new possibilities were opened up. In particular, water relations could now be investigated under controlled climatic conditions.

Tranquillini (1963c) investigated the CO_2 assimilation in relation to air and soil humidity. In water-saturated soil, dry air (25 percent relative humidity) reduced photosynthesis in cembran pines by about 33 percent. A little less water in the soil (half of field capacity) allowed some higher photosynthetic rates. Resistance to dry humidity increases from spring to autumn (Tranquillini 1965).

Pisek and others (1967, 1968, 1969) explored the temperature limits of photosynthesis to chill and frost, and to high temperatures. CO_2 assimilation is operative between -4.7 and $+36^\circ\text{C}$, but the trees can survive temperatures between below -50 and up to 48°C . Of great importance is not only the time factor, but also the physiological condition of the plant. Temperature hardiness changes with the seasons, and young trees or seedlings are more sensitive to extreme temperatures than mature trees. The relation between photosynthetic capacity and temperature was analyzed by Tranquillini and Machl-Ebner (1971). Another factor investigated was day length. Bamberg and others (1967) and Schwarz (1970a, 1970b, 1971) have shown that day length does not influence the photosynthetic capacity during winter depression, but trees kept in warm conditions during winter commenced growth in spring much earlier than plants in nature. The variation in frost resistance of the trees changed in parallel with the temperature. In long-day regimes, frost resistance of cembran pine remained at a lower level than those growing under short-day conditions. The researchers supposed that an endogenous rhythm also influences resistance to extreme temperatures.

Caldwell (1970), using the climatized wind tunnel of the Patscherkofel laboratory, has shown the effect of wind on stomatal aperture, photosynthesis, and transpiration. He did not detect a great influence of low windspeeds on these parameters. At higher windspeeds (up to 8 m/sec) photosynthesis and transpiration were slightly reduced. Baig and others (1974) and Baig and Tranquillini (1980) investigated the cuticular transpiration rate of cembran

pine and found that cuticular transpiration in this tree is very slow but, as in other species, cuticular resistance decreases in parallel to the elevation at which the shoots were collected.

Havranek (1972) found that cold soil temperatures reduce photosynthesis and transpiration in cembran pine. Havranek and Benecke (1978) investigated the influence of soil moisture on transpiration and photosynthesis. Cembran pine begins to close the stomata at a soil water potential of about -0.4 bars. Compared to other species, cembran pine maintains a high water-use efficiency and uses limited soil water economically. Günthardt and Wanner (1982) showed that needles from timberline trees have on the average more wax than those grown at a lower elevation.

Another step to get more precise results for the CO₂ balance of cembran pine was taken by Tranquillini and Schütz (1970). They measured bark respiration at the timberline and reported that bark respiration also shows an annual course. In general, bark respiration of cembran pine was rather high compared to that of other species. The loss of carbon dioxide by stem respiration throughout a year was calculated to be about 18.5 percent of gross photosynthesis. Measuring stem respiration continuously, Havranek (1981) found that there is a marked fluctuation in stem respiration during the growing season, but he could not find any relation between activity of stem respiration and tree ring growth.

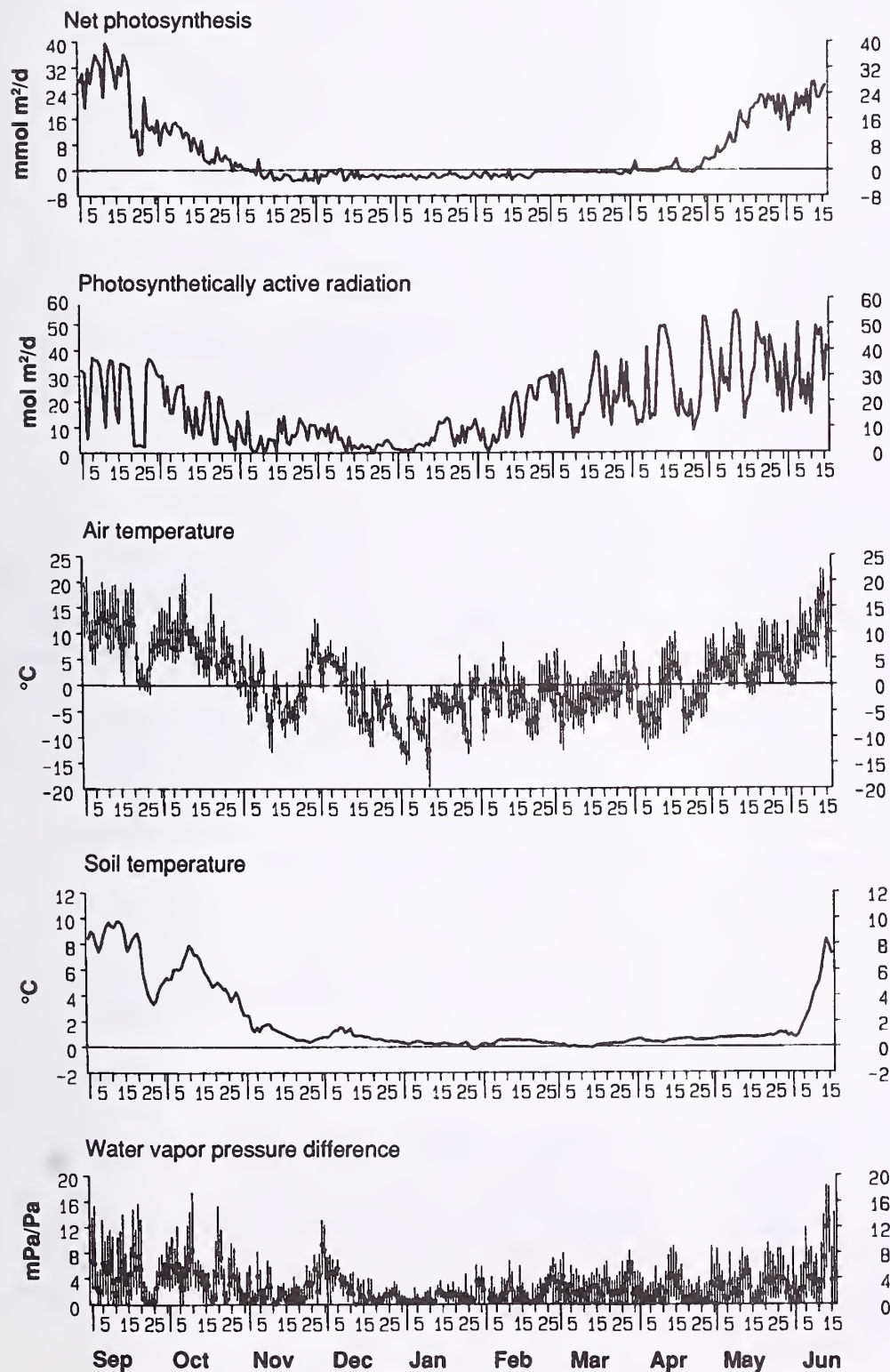


Figure 1—Photosynthesis in cembran pine, photosynthetically active radiation, air and soil temperature, and air humidity measured at the timberline (Stillberg, 1,980 m a.s.l., 1979-80).

FIELD CLIMATE CONTROL

In the late sixties, the thermoelectrically climatized gas exchange chambers were developed by Koch and others (1968). Häsler and Blaser (1981) measured the first daily courses in young cembran pines on the east- and the north-facing slopes of an avalanche gully at the timberline at Stillberg. The two sites exemplify marked differences in microclimate (mean values of soil surface temperatures per growing season differ by more than 10 °C). These differences in microclimate also affect the photosynthetic rates of afforested cembran pines. Carbon dioxide gain, summarized over a season, of the trees on the north-facing slope was 34 percent less than for those on the east-facing slope (Turner and Streule 1983).

Gas exchange measured in combination with meteorological parameters was registered in a branch of an older cembran pine at Stillberg (1,980 m a.s.l.) throughout a whole winter season in 1979-80 (fig. 1). Havranek (1981) published an annual course of growth and a carbon dioxide balance, taken near the Patscherkofel laboratory. During summer the measurements were taken with climatized chambers.

In the middle of the 1980's the so called "forest decline" had high priority in forest research in Europe. The main work in this field was done on other tree species than cembran pine. Nevertheless, some investigations were made on this species. Havranek (1987) took measurements on cembran pine at the timberline to investigate stress caused by air pollution in combination with climatic factors. Genys and Heggstad (1978) did not find a high susceptibility of cembran pines to ozone and sulphur dioxide, but Minarčič and Kubiček (1991) suggested that dust could influence the stomata in needles of cembran pines and thus affect photosynthesis. Lutz and others (1988) analyzed the photosynthetic pigments of cembran pines growing at different altitudes, which thus are exposed to different ozone concentrations. Nebel and Matile (1992) investigated the cause of uncommon yellowing of the needles of cembran pines by analyzing photosynthesis, nutrient relations, longevity, and senescence of these declining needles.

The newest measurements in cembran pine from the Stillberg experimental station are presented in these proceedings (Koike and others). These are probably the first measurements of photosynthesis in cembran pine at the timberline with an artificially elevated atmospheric CO₂ concentration. A detailed publication giving these results is in preparation (Koike and others 1993).

CONCLUSIONS

At the beginning of the research on cembran pine, about 150 years ago, scientists worked mainly at the forest level. With the development of sophisticated measurement instruments, branches, twigs, or even needles were the focus of interest. Rarely did anyone try to extrapolate these results from the small parts to a whole tree, a problem which has still not been satisfactorily resolved. Probably we should try to go back directly to the level of whole trees or even of stands, especially when we want to understand changes caused by external influences, such as air

pollution, rising carbon dioxide, changing UV radiation, and many others.

ACKNOWLEDGMENT

I thank Mrs. M. J. Sieber for critical editing of the English version of my manuscript.

REFERENCES

- Baig, M. N.; Tranquillini, W. 1980. The effect of wind and temperature on cuticular transpiration of *Picea abies* and *Pinus cembra* and their significance in desiccation damage at alpine treeline. *Oecologia*. 47: 252-256.
- Baig, M. N.; Tranquillini, W.; Havranek, W. M. 1974. Cuticuläre Transpiration von *Picea abies*- und *Pinus cembra*-Zweigen aus verschiedener Seehöhe und ihre Bedeutung für die winterliche Austrocknung der Bäume an der alpinen Waldgrenze. *Centralblatt für das gesamte Forstwesen*. 91: 195-211.
- Bamberg, S.; Schwarz, W.; Tranquillini, W. 1967. Influence of daylength on photosynthetic capacity of stone pine (*Pinus cembra* L.). *Ecology*. 48: 264-269.
- Caldwell, M. M. 1970. The effect of wind on stomatal aperture, photosynthesis, and transpiration of *Rhododendron ferrugineum* L. and *Pinus cembra* L. *Centralblatt für das gesamte Forstwesen*. 87: 193-201.
- Cartellieri, E. 1935. Jahresgang von osmotischem Wert, Transpiration und Assimilation einiger Ericaceen der alpinen Zwergstrauchheide und von *Pinus cembra*. *Jahrbücher für wissenschaftliche Botanik*. 82: 460-506.
- Fankhauser, F. 1853. Über das Vorkommen und Gedeihen der Arve. *Schweizerisches Forst Journal*. S 83.
- Fankhauser, F. 1903. Der Kiefernschüttepliz an der Arve. *Schweizerische Zeitschrift für Forstwesen*. 54: 321-323.
- Genys, J. B.; Heggstad, H. E. 1978. Susceptibility of different species, clones and strains of pines to acute injury caused by ozone and sulfur dioxide. *Plant Disease Reporter*. 62(8): 687-691.
- Günthardt, M. S.; Wanner, H. 1982. Die Menge des cuticulären Wachses auf Nadeln von *Pinus cembra* (L.) und *Picea abies* (L.) Karsten in Abhängigkeit von Nadelalter und Standort. *Flora*. 172: 125-137.
- Häsler, R.; Blaser, P. 1981. Nettophotosyntheseaktivität von Arve und Lärche auf verschiedenen Standorten der subalpinen Stufe. *Mitteilungen der forstlichen Bundesversuchsanstalt, Wien*. 140: 179-188.
- Havranek, W. 1972. The influence of soil temperature on photosynthesis and transpiration of young trees and on dry-matter production, at the timber line. *Angewandte Botanik*. 46: 101-116.
- Havranek, W. M. 1981. Stamatmung, Dickenwachstum und Photosynthese einer Zirbe (*Pinus cembra*) an der Waldgrenze. *Mitteilungen der forstlichen Bundesversuchsanstalt, Wien*. 142: 443-467.
- Havranek, W. M. 1987. Physiologische Reaktionen auf Klimastress bei Bäumen an der Waldgrenze. Symposium Klima und Witterung in Zusammenhang mit den neuartigen Waldschäden. Tagungsbeiträge, München: 115-138.

- Havranek, W. M.; Benecke, U. 1978. The influence of soil moisture on water potential, transpiration and photosynthesis of conifer seedlings. *Plant and Soil*. 49(1): 91-103.
- Holzer, K. 1958. Die winterlichen Veränderungen der Assimilationszellen von Zirbe (*Pinus cembra* L.) und Fichte (*Picea excelsa* Link.) an der alpinen Waldgrenze. *österreichische botanische Zeitschrift*. 105: 323-346.
- Keller, C. 1890. Tierische Forstbeschädigungen an der Arve. *Österreichische Forstzeitung*: 267-268.
- Keller, C. 1901. Die Arven-Erkrankungen im Oberengadin. *Schweizerische Zeitschrift für Forstwesen*. 52: 293-299.
- Keller, C. 1910. Die tierischen Feinde der Arve. *Schweizerische Centralanstalt für forstliches. Versuchswesen, Mitteilungen*. 10(1): 1-50.
- Keller, T. 1970. Über die Assimilation einer jungen Arve in Winterhalbjahr. *Bündnerwald*. 23(2): 49-54.
- Keller, T.; Beda-Putz, H. 1973. Gas exchange of leafless shoots in winter. *Schweizerische Zeitschrift für Forstwesen*. 124(6): 433-441.
- Kerner, A. 1866. Wachstumsbedingungen der Zirbe. *österr. Monatsschr. Forstwesen*. 1-15.
- Koch, W.; Klein, E.; Walz, H. 1968. Neuartige Gaswechsel-Messanlage für Pflanzen in Laboratorium und Freiland. *Siemens Zeitschrift*. 42: 392-404.
- Koike, T.; Häslar, R.; Matyssek, R.; Item, H. 1993. Seasonal changes in the photosynthetic capacity of *Larix decidua* and *Pinus cembra* planted on contrasting slopes at the timberline at Stillberg (Davos), eastern Switzerland. [In preparation].
- Kronfuss, H. 1980. Das Bestandesklima einer Hochlagenaufforstung auf einem Sonnenhang. In: Beiträge zur subalpinen Waldforschung. 2. Folge. Mitteilungen der forstlichen Bundesversuchsanstalt, Wien. 129: 81-103.
- Kronfuss, H. 1983. Das Höhenwachstum einer Zirbenaufforstung auf einem Südhang in klimatologischer Sicht. *Allgemeine Forstzeitung*. 94(12): 330-332.
- Kronfuss, H. 1986. Die Abhängigkeit des Höhenzuwachses der Zirbe von der Seehöhe. Jahresbericht 1985. Forstliche Bundesversuchsanstalt, Wien: 137-144.
- Lutz, C.; Schulte-Hostede, S.; Kirchner, M.; Reuther M. 1988. Photosynthetische Pigmente aus Nadelbäumen unterschiedlicher Höhenstufen des Ötztals. Internationales Symposium "Verteilung und Wirkung von Photooxidantien im Alpenraum. Sitzungsberichte München 1988: 415-425.
- Minarčič, P.; Kubíček, F. 1991. Localization of emissions on the needle surface. 1. Methodology, morphological characterization of the stomata (*Picea abies*, *Pinus cembra*). *Ekologia, CSFR*. 10(4): 405-413.
- Nebel, B.; Matile, Ph. 1992. Longevity and senescence of needles in *Pinus cembra*. *Trees*. 6(3): 156-161.
- Nevole, J. 1914. Die Verbreitung der Zirbe in der österr.-ungar. Monarchie. Verlag W. Frick Wien. 89 p.
- Pisek, A.; Winkler, E. 1958. Assimilationsvermögen und Respiration der Fichte (*Picea excelsa* Lind.) in verschiedener Höhenlage und der Zirbe (*Pinus cembra* L.) an der alpinen Waldgrenze. *Planta*. 51: 518-543.
- Pisek, A.; Winkler, E. 1959. Licht- und Temperaturabhängigkeit der CO₂-Assimilation von Fichte (*Picea excelsa* Lind.), Zirbe (*Pinus cembra* L.) und Sonnenblume (*Helianthus annuus* L.). *Planta*. 53: 532-550.
- Pisek, A.; Larcher, W.; Moser, W.; Pack, I. 1969. Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. III. Temperaturabhängigkeit und optimaler Temperaturbereich der Netto-Photosynthese. *Flora B*. 158(3): 608-630.
- Pisek, A.; Larcher, W.; Unterholzner, R. 1967. Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. I. Temperaturminimum der Nettoassimilation, Gefrier- und Frostschaadenbereiche der Blätter. *Flora B*. 157(1): 239-264.
- Pisek, A.; Larcher, W.; Unterholzner, R.; Pack, I. 1968. Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. II. Temperaturmaximum der Netto-Photosynthese und Hitzeresistenz der Blätter. *Flora B*. 158(2): 110-128.
- Rikli, M. 1909. Die Arve in der Schweiz. *Neue Denkschr. Schweizerische naturforschende Gesellschaft*. 44. 455 p.
- Schönenberger, W.; Frey, W., eds. 1988. Untersuchungen zur Ökologie und Technik der Hochlagenaufforstung. Forschungsergebnisse aus dem Lawinenanrissgebiet Stillberg. *Schweizerische Zeitschrift für Forstwesen*. 139(9): 735-820.
- Schwarz, W. 1970a. Der Einfluss der Photoperiode auf das Austreiben, die Frosthärte und die Hitzeresistenz von Zirben und Alpenrosen. *Flora*. 159: 258-285.
- Schwarz, W. R. 1970b. Frost hardiness, resistance to heat, and CO₂ uptake in seedlings and mature stages of *Pinus cembra* L. Proc. 3. Forest Microclimate Symposium, Kananaskis Forest Experimental Station; 1969; Seebe, AB: 137-145.
- Schwarz, W. 1971. The photosynthetic capacity of some evergreens during the winter and the speed of their recovery of activity after sharp frosts. *Berichte der deutschen botanischen Gesellschaft*. 84(10): 585-594.
- Simony, F. 1870. Die Zirbe. *Jahrbuch des österreichischen Alpenvereins*. 6: 349-359.
- Tranquillini, W. 1955. Die Bedeutung des Lichtes und der Temperatur für die Kohlensäureassimilation von *Pinus cembra*-Jungwuchs an einem hochalpinen Standort. *Planta*. 46: 154-178.
- Tranquillini, W. 1957. Standortsklima, Wasserbilanz und CO₂-Gaswechsel junger Zirben (*Pinus cembra*) an der alpinen Waldgrenze. *Planta*. 49: 612-661.
- Tranquillini, W. 1958. Die Frosthärte der Zirbe unter besonderer Berücksichtigung autochoner und aus Forstgärten stammender Jungpflanzen. *Forstwissenschaftliches Centralblatt*. 77: 89-105.
- Tranquillini, W. 1959a. Die Stoffproduktion der Zirbe an der Waldgrenze während eines Jahres. *Planta*. 54: 107-129.
- Tranquillini, W. 1959b. Die Stoffproduktion der Zirbe (*Pinus cembra* L.) an der Waldgrenze während eines Jahres. II. Zuwachs und CO₂-Bilanz. *Planta*. 54(2): 130-151.

- Tranquillini, W. 1963a. Der Jahresgang der CO₂-Assimilation junger Zirben. Mitteilungen der forstlichen Bundesversuchsanstalt, Wien. 60: 501-534.
- Tranquillini, W. 1963b. Die CO₂-Jahresbilanz und die Stoffproduktion der Zirbe. Mitteilungen der forstlichen Bundesversuchsanstalt, Wien. 60: 535-546.
- Tranquillini, W. 1963c. Die Abhängigkeit der Kohlen-säureassimilation junger Lärchen, Fichten und Zirben von der Luft- und Bodenfeuchte. Planta. 60: 70-94.
- Tranquillini, W. 1963d. Über die Frostresistenz der Zirbe. Mitteilungen der forstlichen Bundesversuchsanstalt, Wien. 60: 547-562.
- Tranquillini, W. 1965. Über den Zusammenhang zwischen Entwicklungszustand und Dürre-resistenz junger Zirben (*Pinus cembra* L.) im Pflanzgarten. Mitteilungen der forstlichen Bundesversuchsanstalt, Wien. 66: 241-271.
- Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Berlin: Springer-Verlag. 137 p.
- Tranquillini, W.; Machl-Ebner, I. 1971. Über den Einfluss von Wärme auf das Photosynthesevermögen der Zirbe (*Pinus cembra* L.) und der Alpenrose (*Rhododendron ferrugineum* L.) im Winter. Report of the Kevo Subarctic Research Station. 8: 158-166.
- Tranquillini, W.; Schütz, W. 1970. Über die Rinden-atmung einiger Bäume an der Waldgrenze. Centralblatt für das gesamte Forstwesen. 87: 42-60.
- Turner, H.; Streule, A. 1983. Wurzelwachstum und Sprossentwicklung junger Koniferen im Klimastress der alpinen Waldgrenze, mit Berücksichtigung von Mikroklima, Photosynthese und Stoffproduktion. Irnding, Austria: Bundesanstalt Gumpenstein: 617-635.
- Ulmer, W. 1937. Über den Jahresgang der Frosthärte einiger immergrüner Arten der alpinen Stufe, sowie der Zirbe und Fichte. Jahrbücher für wissenschaftliche Botanik. 84: 553-592.

A PATTERN OF *PINUS PUMILA* SEED PRODUCTION ECOLOGY IN THE MOUNTAINS OF CENTRAL KAMTCHATKA

Peter A. Khomentovsky

Abstract—This paper discusses the results of *Pinus pumila* cone production studies in the mountains of central Kamtchatka. *Pinus pumila* was found to have a very high seed production potential when not overtopped by neighboring trees. When shaded, few or no cones were produced on *P. pumila*. Seed production was not significantly dependent on altitude and site conditions. However, elevations above 1,300-1,400 m were unfavorable for cone survival, mainly because of low temperature and phenological delay. Successful seed production requires snow cover to protect ovulate buds on low-lying branches from freezing in the winter. In the summer, good seed production is related to high insolation, wind protection on cold sites, absence of shading, and good drainage for the root systems. At midelevations, under good seed production conditions in Kamtchatka, about 110 kg of seeds per hectare will be produced as compared to only 1 kg at the upper elevational limits. *Pinus pumila* appears to have a high evolutionary potential that reveals itself in prominent and wide polymorphism of reproductive organs.

The main purpose of this paper is to give a brief description of some reproductive characteristics and ecological features of typical subalpine dwarf pine (*Pinus pumila* [Pall.] Regel) (Pinaceae, Strobilus) (Pp) for many regions of its area ecotopes of the central Kamtchatka Mountains in northeastern Asia (fig. 1).

Some years ago, we tried to identify the response of seed production (reflected in cones, seed, and nuclei masses and sizes) to some of the most evident differences of Pp environments, mainly to ecotopes, altitudinal position, and their location in regions with maritime or continental climate. We noticed (Khomentovsky and Khomentovskaya 1990) that there is no strong dependence of seed parameters and cone crop on the ecotope, elevation, and its position in the relief. Pp was supposed to have some ecotopic (macro- or microclimatic) optimum of seed production, which could be indirectly characterized by the climate within the belt of 600 to 900 m above sea level in the interior continental climate regions of Kamtchatka peninsula, and widened in its lower limit almost to sea level near the coast.

At the same time we tried to develop some of the first descriptions of conophagous insects feeding on Pp and to

define their role in cone crop size and quality variation. We found (Khomentovsky and Efremova 1991) that the only two presently known insect species inhabiting Pp cones are *Cecidomyia pumila* Mamaev and Efremova (Diptera, Cecidomyiidae) and *Eupithecia abietaria* Goeze (Lepidoptera, Geometridae) (the taxonomy of the last species has to be rechecked), and they affect crop quality very little. Therefore, this damage could be treated as negligible or at least not proven to be important.

These preliminary conclusions forced us to proceed with a more detailed investigation of Pp seed production. Having no possibilities for obtaining direct microclimatic information, we decided to define possible principal responses of Pp seed production to elevation and ecotopical features within a small creek basin with a high altitudinal gradient.

THE RESEARCH AREA

The research area is situated almost in the geographical center of the Kamtchatka (56 °N., 158 °E.), in the Sredinnij Mountain Range system, the main system in the peninsula (fig. 1). According to the botanical-geographical regionalization scheme of L. F. Kunitsin (1963), this territory is included in the "mountain above alpine tundra shrubby region." According to our scheme (Khomentovsky and others 1989), it lies in the contact area of "Central Kamtchatka plainland-submountain province of conifer-stonebirch forests" and "Sredinno-Western middle mountain stone birch-tundra forest province." The area covers the upper part of the conifer forest vegetation belt, subalpine, alpine, and above-alpine belts in Kamtchatka (figs. 1 and 2).

Climate is subcontinental, with 300 to 400 mm of annual precipitation, moderately cold and snowy winters, and cool summers (monthly average air temperature in Esso village is 3 °C in May, 9.5 °C in June, 13 °C in July, 12 °C in August, and 6 °C in September. The permanent snow cover at elevations of 700 m and higher begins to accumulate in the first half of October and disappears mainly in May.

Orographically, the area can be called "typical middle altitudinal-mountainous" (according to common understanding), which for Kamtchatka actually means middle and high mountains (due to the compression of its altitudinal vegetation belts). Average height of the mountains is about 1,500 m. Geological and geomorphological structure of the area is determined by volcanogenic basalts and andesites (Q1, Q2, Q4), and by quaternary glacial, fluvio-glacial (Q3), alluvial, and proluvial (Q4) deposits. Glacial relief is conspicuous, especially in the upper parts of river

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Peter A. Khomentovsky is Head of the Biogeocenology Laboratory, Kamtchatka Institute of Ecology and Nature Management, Prospect Rybakov, 19-A, Petropavlovsk-Kamtchatsky 683024 Russia.

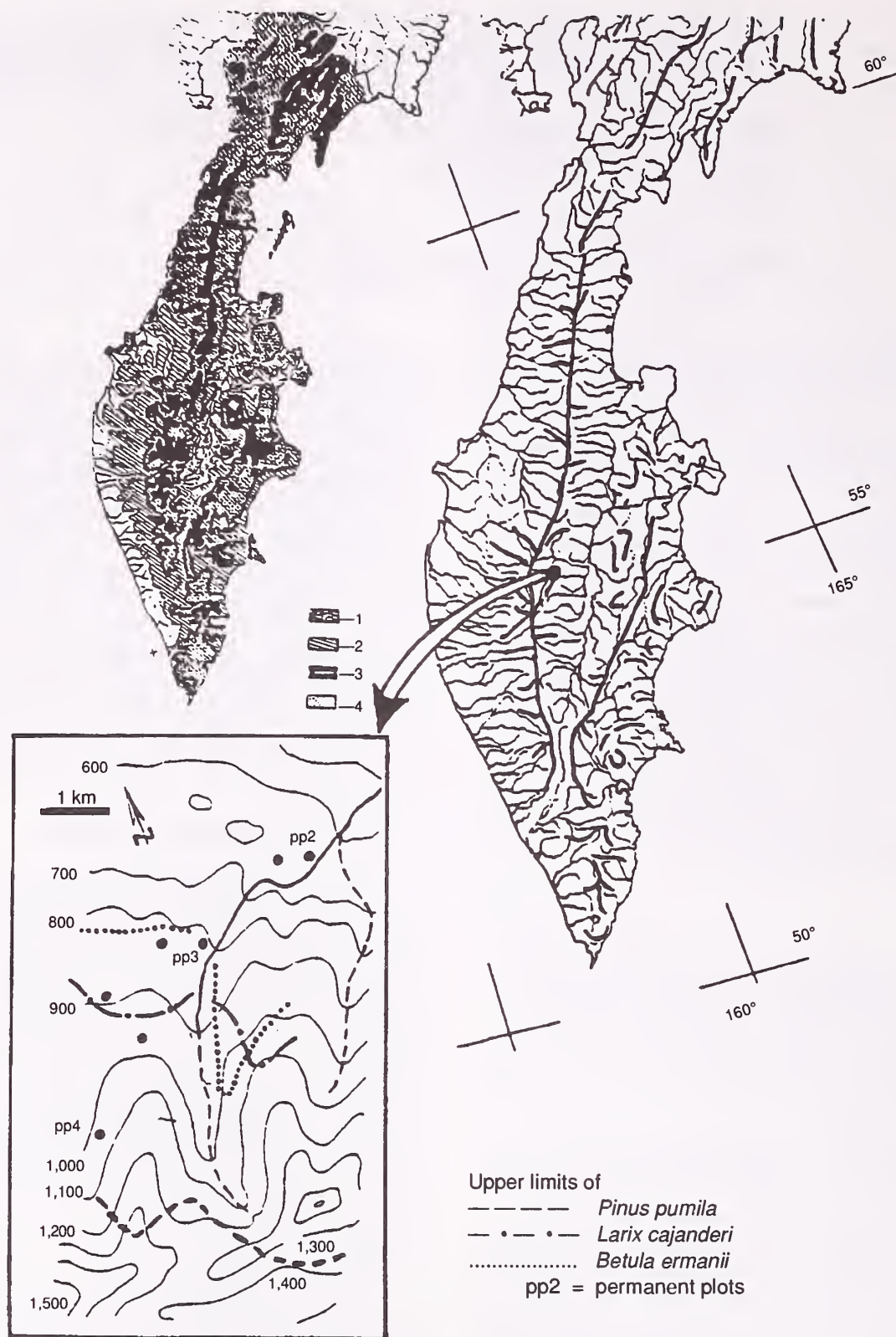


Figure 1—General description of the research area in Kamtchatka peninsula. Top left: principal scheme of vegetation belts: 1—subalpine, 2—boreal forest, 3—alpine, 4—coastal and lowland. Top right: main mountain ridges and hydrological net. Bottom left: research area, within small basin. Dots are points where material was collected.

and creek basins. Soils are typical for the Kamtchatka Mountain regions classification (I. A. Sokolov 1973), with the additions by N. V. Kazakov (personal communication). They include turf illuvio-humus, turf illuvio-volcanic ash, tundra illuvio-humus, tundra illuvio-humus-volcanic ash, and turf primitive. Soil genetics reveal themselves in the existence of specific features including the long-term freezing period, anaerobic reactions in the lower horizons, and

more or less permanent (on large time scale) weak or moderate volcanic ashfalls impacts (mainly from the eastern part of peninsula).

Due to the geographical position, mountain relief, and severe climate of the area, vegetation is not very diverse and exhibits a mosaic-like spatial pattern. River valleys and lower parts of their tributaries are occupied by *Populus suaveolens*, *Chosenia arbutifolia*, *Larix cajanderi*,

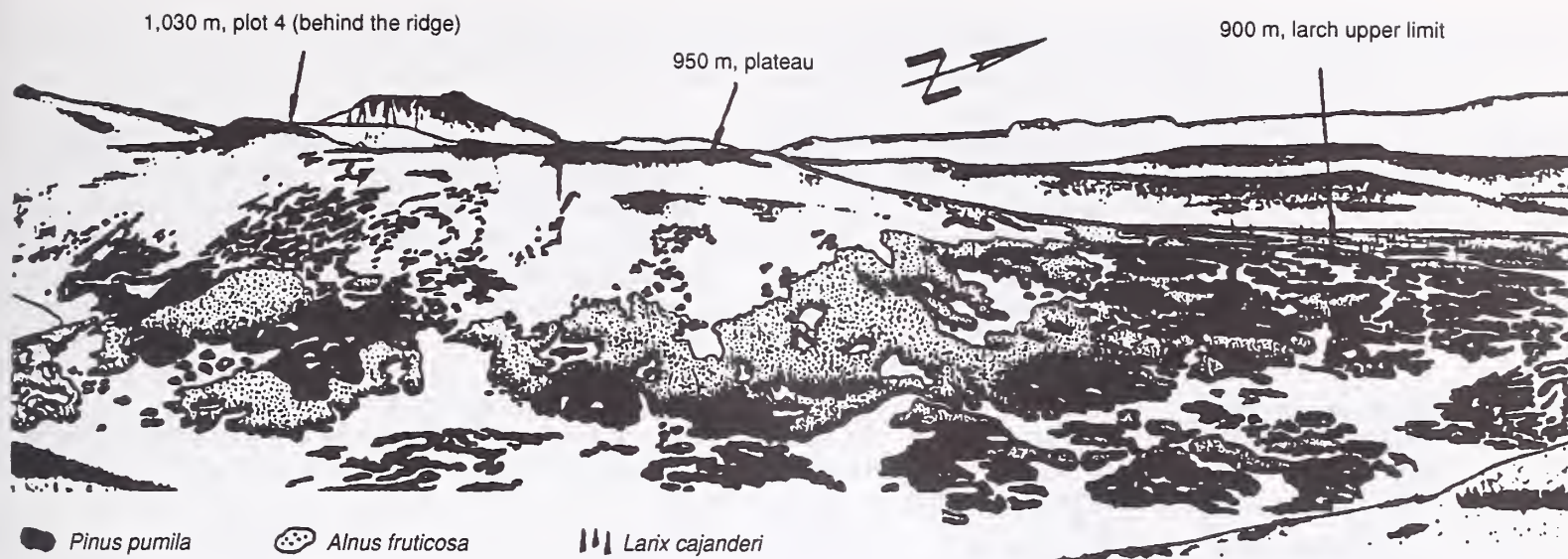


Figure 2—A fragment of the vegetation cover in the upper part of the altitudinal transect (see also fig. 1).

Betula kamtschatica, and *B. ermanii*. Two dwarf tree species, *Pinus pumila* and *Alnus kamtschatica*, are widely spread along the whole vegetation profile. They occur by groups or strips along the moraine tongues, river terraces, fluvoglacial deposits, and watershed ridges and slopes, and form the upper limit of woody vegetation (fig. 2).

Plant formations in the middle and high altitudes are almost the same (except for *Populus* and *Chosenia*), but, moving upward along the narrowing valleys and watersheds, along the altitudinal environmental gradient of gradually decreasing plant life conditions, we can see the distribution pattern of the formation changing from "macromosaic" to "micromosaic." Tree distribution is more strictly related to soil temperature conditions and drainage gradients, and to sites sheltered from wind and snow abrasion. This is true even for such ecologically flexible dwarf species as *Pinus pumila* and *Alnus kamtschatica*.

The upper elevational limits of upright-growing woody vegetation (*Larix kamtschatica*, *Betula ermanii*) are located between 900 to 1,000 m, depending on site conditions. *Pinus pumila* and *Alnus kamtschatica* occur up to 1,300 to 1,400 m (rare clumps). Up to 1,200 m *P. pumila* is able to produce seeds.

MATERIALS AND METHODS

Data were gathered mostly in September to October 1990 (with some additional data from other years) at the field base "Bolgit," in the vicinity of Esso village (Bistrinsky district of Kamtschatka region), in the "Tupikin clyutch" creek basin, within an area of about 10 km². This paper presents the material from one slope exposed to the east-northeast and from the area nearest to the watershed (up to 50 m from the slope edge), within an altitudinal range of 650 to 1,030 m. Permanent plots on an existing transect and some additional temporary points were chosen for the cone crop measuring and sampling (fig. 1).

The following information was collected on each sample site (table 1): type of plant community, topographic

location and ground cover of Pp clumps, average seasonal height of skeleton branches, general moisture conditions, shading by neighboring upright trees or clumps.

EXPLANATORY COMMENTS

First, strictly speaking, we cannot consider Pp plants as common trees—they are not standing separately and do not have a single trunk; in most cases they overlap each other, both aboveground and in underground parts. Also, we cannot call them "clones" because we do not know their origin and level of genetic relationships—which is especially important in the case of seed dispersal by animals. The best term would be "clump" (we are grateful to Dr. Diana Tomback for some explanations on this topic).

Second, the single trunk (in traditional understanding) of Pp is considered a creeping tree not a bush, and its length is only several centimeters or tens of centimeters. Branches of first and second order (I prefer to call them "trunk-branches") exhibit the same physiognomy, bear similar quantity of shoots, and form multitrunck-like crowns. In the case of syngenetic origin and continuous dispersal, Pp plants form such dense cover by overlapping basal parts in the litter and root systems that it is impossible to identify single plants and thus their total numbers without destroying the stand. This forced us to use the only acceptable method of measuring cone crops or similar parameters—instead of measuring only one tree or clump, measure by square unit such as hectares or square meters. Certainly, the stand structure and characteristics of ground cover have to be taken into account, especially for practical taxation.

Third, it is also impossible, in many cases, to determine real age of adult Pp plants. They produce adventitious roots, are growing apically, and are gradually decaying in their basal parts during most of their lifetime, theoretically endlessly. We have to recognize that we really can only know the age at the moment of measuring, similar to being counted in young trees, and not the real one, which is usually higher.

Table 1—Short description of the ecotopes and *Pinus pumila* clumps being analyzed. The age of clumps in these analyses lies between 150 and 260 years¹

Altitude, m asl	Position in the relief	<i>Pinus pumila</i> community type	Way of main water supply	Woodstand composition	<i>Pinus pumila</i>		Shading	
					H avg, cm	SC, %	UTr	Ppc
1,030	Upper part of the flat watershed, shaded from S and E by the ridge	<i>Pumilae pinetum carioso-hypnoso-ericosum</i> , with fragments of <i>P.p. cladinosum</i> (CHE* ¹ C)	A+S	10Pp	100 (15-20)	80 unev	0	1
950	Plateau, opened to all directions, watershed with slight slope to NNE	<i>P.p. purum</i> , with fragments of <i>P.p. carioso-cladinosum</i> (P* ¹ CC)	A	10Pp	40 (10-15)	40 unev	0	0
900	Flat watershed above the creek source, shaded by the ridge from S	<i>P.p. hypnoso-carioso-ericosum</i> (HCE)	A+S	10Pp+Lk (upper limit of Lk)	300	40 unev	1	1
810	A ridge of the complex watershed, slight slope to the NE	<i>P.p. carioso-hypnoso-ericosum</i> (CHE)	A	10Pp+Lk	150 (35-40)	60 unev	1	2
800	Middle part of the E exposed slope of wide creek valley	<i>P.p. hypnoso-carioso-ericosum</i> (HE)	S+A	10Pp+Lk	200	80	0	1
680	Eastern border of the watershed ridge with flattened top	<i>P.p. hypnoso-carioso-ericosum</i> (HCE)	A+S	7Pp 3Lk	300	60 unev	2	1
650	Lower part of E exposed slope in narrow creek valley	<i>P.p. ericoso-sphagnosum</i>	S	10Pp+Ak	300 (40-45)	100	0	3

¹*Pinus pumila* community type: in parentheses—abbreviation for fig. 8; Way of main water supply: A—atmospheric, S—slope; Woodstand composition: Pp—*Pinus pumila*, Lk—*Larix cajanderi*, Ak—*Alnus kamtschatica* (dwarf alder); *Pinus pumila*: H avg—average height (cm), in parentheses—rough estimation of annual shoot elongation (mm); SC%—surface covering by the clumps, "unev"—uneven; Shading: UTr—from upright trees of different species, Ppc—from *Pinus pumila* neighboring clumps; 0—no shading, 1—slight, 2—moderate, 3—heavy shading.

In each point for data and sample collecting we used 3 to 5 small randomized plots of different size—from 1 to 15 m². The following parameters were countered in place (table 2): number of skeleton branches ("trunk-branches"), number of germinating shoots on each skeleton branch; number of current year crop cones (the second year of cone development) and number of next year crop cones (female buds of the first year) on each germinating shoot and each skeleton branch; and among the total quantity of each year's cones the number of cones damaged by insects (*Cecidomyia pumila*—damage in the first year of cone development, *Eupithecia abietaria*—damage in the second year of cone development), and by the nutcracker (*Nucifraga caryocatactes kamtschatkensis*).

At each site, 10 to 100 cones of the current year's crop were collected and measured before they dried (cone length and cone diameter). Later, after air drying during some weeks or months, cones and seeds were measured by 16 other parameters, six of which are discussed in this paper: cone mass; 1,000 seeds mass; 1,000 nuclei mass (both by measuring a number of samples with 50 seeds in each); number of seed scales in the cone; among the total

number of seed scales, the number of scales not containing seeds under them; and total seed quantity in the cone.

RESULTS AND BRIEF COMMENTS

- The structure of the cone-bearing portion of the crown and cone crop estimates (tables 1 and 2, figs. 1-6):

As a whole, the number of skeleton branches and germinating shoots per hectare varied very little within altitudes of 650-800 m and definitely increased upward. This could be explained by increasing isolation. Most likely it was the reason for the especially increasing number of germinating shoots (two to three times higher than skeleton branches) and, correspondingly, the numbers of current-year and next-year cones. The last varied more than the first because some of them will inevitably die in the natural selection process during the maturation time in the coming year.

The number of shoots with cones per skeleton branch (fig. 4) changed opposite to that of the number of skeleton branches per 1 hectare (we noticed the increased number

of shoots, including nongerminating). Even a slight plant shading immediately resulted in a change in the number of shoots (sites 900 m and 1,030 m).

The quantity of current and next-year crop cones per one germinating shoot had specific dispersal features: at each site, especially in the lower, shaded part of the elevation profile, cones of any one year were overwhelming. This migration of intensive seed-producing centers from year to year supports our previous conclusion

(Khomentovsky and Efremova 1991) about the existence of local seed production mosaics, which provides a continuous supply of seeds, important not only for guaranteed reproduction and microevolutionary diversity for Pp, but also for all zooconsumers such as nutcracker, other birds, and mammals.

- Cones and seeds mass and size variation (tables 1, 3; figs. 7 and 8):

Table 2—Characteristics of germinating crown parts and cone crop outcome of *Pinus pumila* in central Kamchatka Mountains¹

nn	Parameter	Altitude (m above sea level)						
		650	680	800	810	900	950	1,030
1	No. of skeleton branches/ha	1,200	4,167	2,240	21,111	11,000	30,000	10,333
2	No. of germinating shoots/ha	1,733	7,917	3,200	47,778	57,000	86,667	33,000
3	No. of this year crop cones/ha	1,733	4,375	3,136	2,389	46,170	56,334	28,000
4	No. of next year crop cones/ha	260	0	160	51,122	19,950	143,000	24,550
5	No. of germinating shoots/skel. bran.	1.44	1.90	1.43	2.26	5.19	2.89	3.00
6	No. of this year crop cones/skel. bran.	1.44	2.00	1.40	0.11	4.20	1.88	2.56
7	No. of next year crop cones /skel. bran.	0.22	0	0.07	2.42	1.82	4.77	2.54
8	No. of this year crop cones/germ. shoot	1.00	1.05	0.98	0.05	0.81	0.65	0.76
9	No. of next year crop cones/germ. shoot	0.15	0	0.05	1.07	0.35	1.65	0.86
10	Percentage of skeleton branches with various numbers of germinating shoots:							
	with one shoot	67	30	64	58	28	22	32
	with two shoots	22	50	29	16	18	34	33
	with three shoots	11	20	7	16	0	22	8
	with four shoots	0	0	0	0	9	11	4
	with five shoots	0	0	0	5	9	0	8
	with six shoots	0	0	0	0	0	0	2
	with seven shoots	0	0	0	0	0	0	5
	with eight shoots	0	0	0	0	9	11	5
	with nine shoots	0	0	0	0	9	0	0
	with ten shoots	0	0	0	0	0	0	2
	with eleven shoots	0	0	0	0	0	0	0
	with twelve shoots	0	0	0	5	0	0	0
	with thirteen shoots	0	0	0	0	9	0	1
11	Percentage of germinating shoots bearing various number of this year cones (T) and next year cones (N):							
	0N - 1T	81	100	93	86	63	8	32
	0N - 2T	7	0	2	8	4	0	6
	Cumulative percent of shoots with this year's crop cones only	88	100	95	94	67	8	38
	1N - 0T	4	0	0	3	25	15	30
	2N - 0T	4	0	5	0	2	11	7
	3N - 0T	0	0	0	0	0	11	0
	Cumulative percent of shoots with this year's crop cones only	8	0	5	3	27	37	37
	1N - 1T	4	0	0	3	3	23	10
	1N - 2T	0	0	0	0	3	4	2
	2N - 1T	0	0	0	0	0	15	6
	2N - 2T	0	0	0	0	0	5	5
	3N - 1T	0	0	0	0	0	8	1
	4N - 1T	0	0	0	0	0	0	1
	Cumulative percent of shoots with cones of both years	4	0	0	3	6	55	25

¹Only the area covered with *Pinus pumila* clumps is taken into account (par. 1-4), not the whole territory of the site; number of next-year cones can decrease during the year due to natural selection processes.

Table 3—Some characteristics of *Pinus pumila* cones and seeds in various elevations in central Kamchatka Mountains (within research area)¹

Regression on altitude	Correlation	Average value
CL = 54.71 - 0.020 A	R = -0.73	AVG (cl) = 43 +/- 8 (25-62)
CD = 33.68 - 0.010 A	R = -0.79	AVG (cd) = 27 +/- 2 (18-37)
CM = 7.81 - 0.030 A	R = -0.41	AVG (cm) = 7 +/- 1 (4-10)
SSN = 32.30 + 0.010 A	R = 0.53	AVG (ssn) = 39 +/- 5 (26-52)
SWS = 9.06 + 0.004 A	R = 0.33	AVG (sws) = 11 +/- 3 (5-18)
SQT = 28.50 + 0.003 A	R = 0.76	AVG (sqt) = 45 +/- 5 (26-68)
SMP = 46.71 + 0.002 A	R = -0.11	AVG (smp) = 45 +/- 3 (32-55)
SMTH = 101.67 - 0.020 A	R = -0.45	AVG (smth) = 84 +/- 8 (52-116)
NMTH = 56.49 - 0.020 A	R = -0.49	AVG (nmth) = 43 +/- 4 (27-68)

¹CL—cone length, mm; CD—cone diameter, mm; CM—cone mass, g; A—altitude, m above sea level; SSN—seed scale number; SWS—number of scales without seeds (within SSN); SQT—total number of seeds in the cone; SMP—percentage of seeds mass in cone mass; SMTH—mass of 1,000 seeds, g; NMTH—mass of 1,000 nuclei, g. In parentheses at the right side—minimum and maximum values.

Mass variation (here and later we speak about current-year crop cones only) is more evident in the upper part of the elevation profile, in micromosaic sites with increasing abiotic environmental pressure. In sufficiently insolated (sunny) and wind-protected sites cone mass is increasing, in shaded sites or windy plateaus—decreasing. At the upper elevation levels of Pp distribution (1,200-1,300 m) we observed natural abrupt decreases of all seed-producing parameters. It is remarkable that in general cones and seeds masses are not too closely related to definite altitudinal or site positions of the tree, even in cases of evidently unfavorable environments (site 950 m).

Self regulation of seed production is obvious also: along the elevation gradient, number of seed scales in the cone

(with and without seeds) and total number of seeds in the cone slightly increases as well, and at the same time seed and nuclei mass is unchanging or slightly decreasing. It means that seeds become smaller but grow in quantity, keeping the same reproduction potential and having more protection from environmental impacts.

Cone size variation, most evident in their length, corresponds with mass variation in relation to site position in the landscape. Here, as well as in the previous case, the main impact factor is not elevation but landscape structure of the ecotope (slopes in wide or narrow valley, plateau, watershed ridge, etc.). Biocenotic structure is not too important in this case, at least at the forest type level. All ecotopes, excluding the 950-m site (opened plateau),

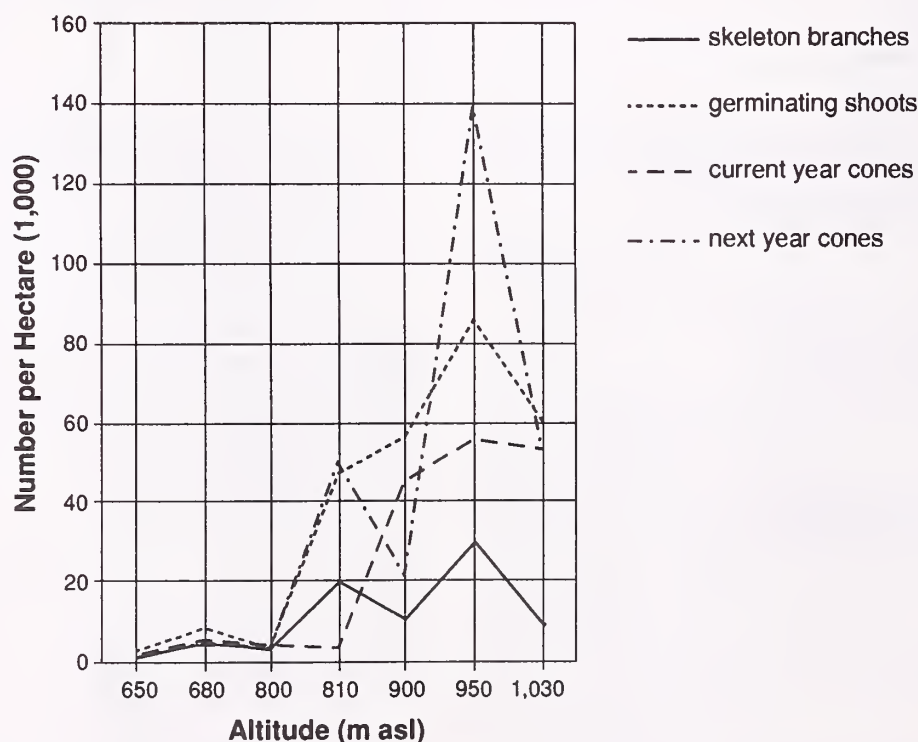


Figure 3—Principal structure of *Pinus pumila* crowns at various altitudes and estimated cone crop per hectare.

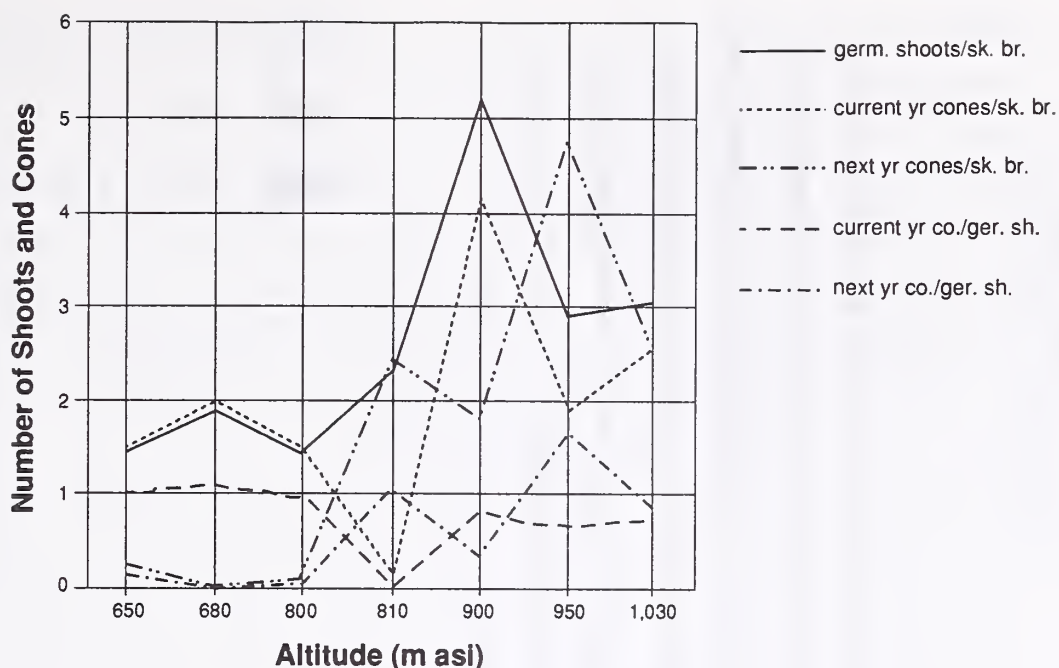


Figure 4—Structure of *Pinus pumila* crown germinating part (number of germinating shoots and estimated cone crop per skeleton branch).

are occupied by the same group of forest types—*Pumilae pinetum carioso-hypnoso-ericosum*, and its variations. Generally speaking, cones size, as well as cones mass, which has good correlation with them ($r = 0.7-0.8$), vary within limits already known for the species.

- Damage caused by insects and birds (fig. 9):

This was investigated in some detail previously (Khomentovsky and Efremova 1991) and is not likely

to effect any substantial change in average cone sizes: it does not affect cone diameter and leads to cone length decreases up to 3-9 percent (*Cecidomyia pumila*). However, in some cases this insect species damage results in underdevelopment of up to 20 percent of the seeds, but this impact usually does not stop the development of the rest of the seeds in the cone and is compensated at the population level by the abundant production of seeds.

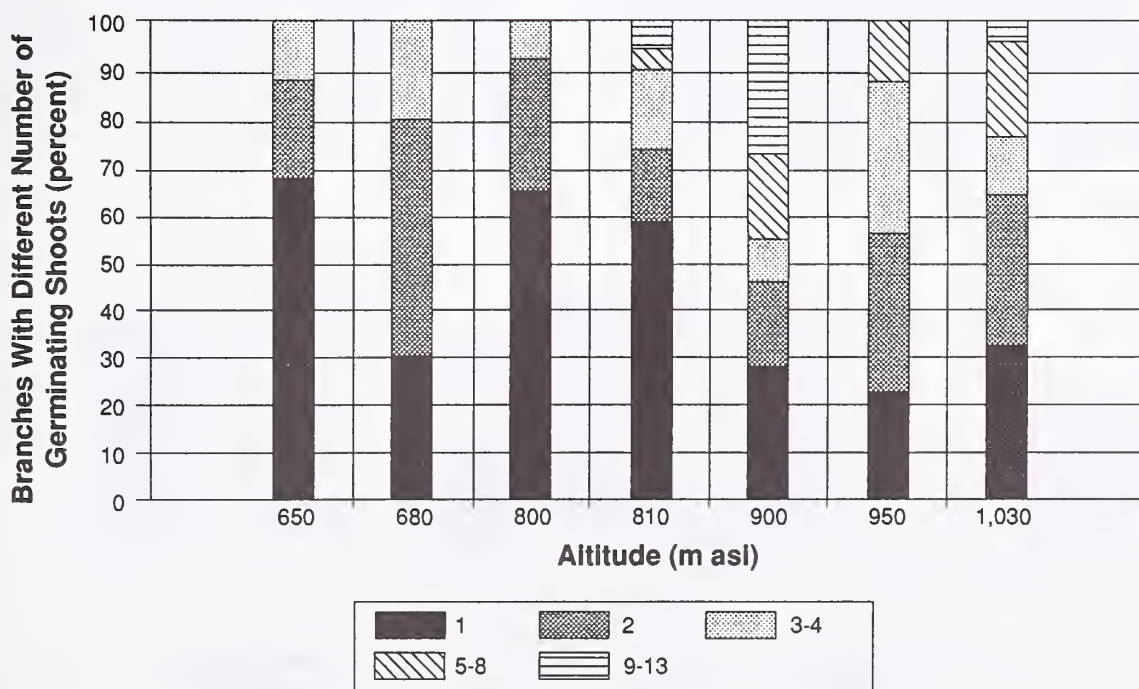


Figure 5—Germinating shoots quantity distribution on skeleton branches.

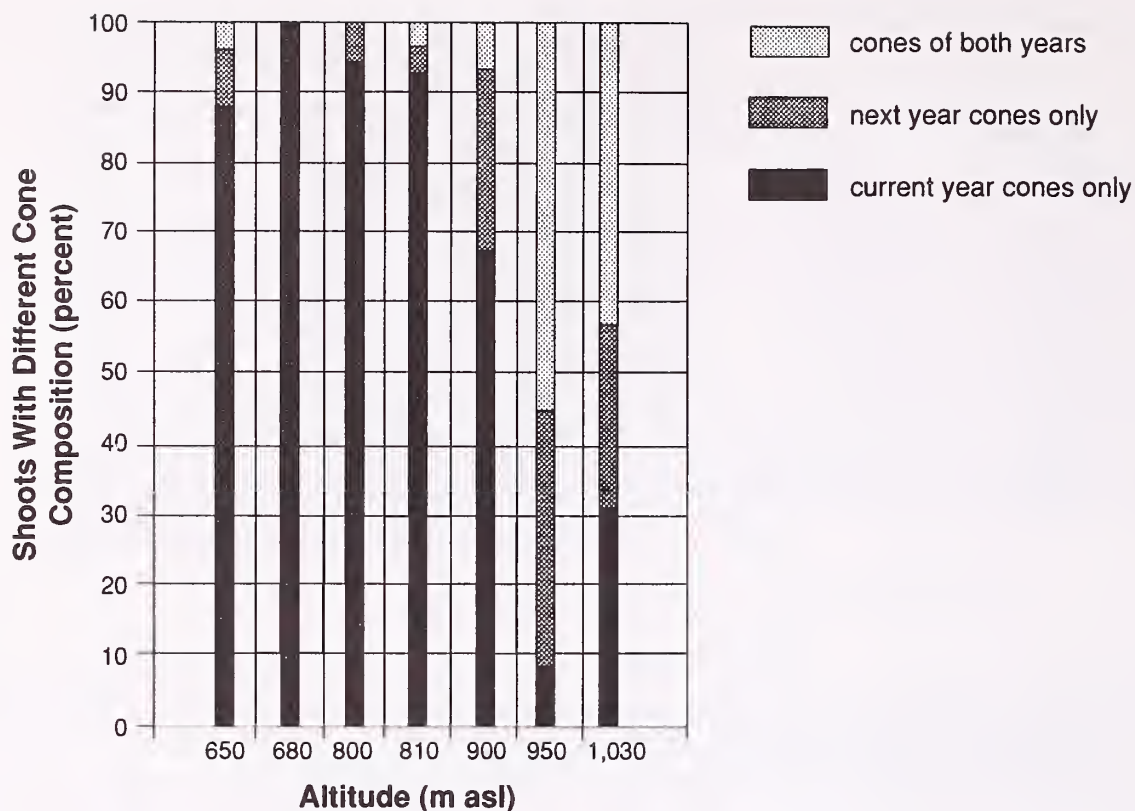


Figure 6—Distribution of current-year and next-year cone crop on germinating shoots.

The level of damage caused by *Cecidomyia pumila*, clearly noticeable visually by the cone curving, is usually rather high everywhere but it varies with different site, environmental, and weather conditions, to which insects are more sensitive. In our case it was changing from moderate damage of 25-50 percent on the 650-m site (slope in the narrow valley), the 800-m site (slope in the wide

valley), and the 900-m site (wind-protected watershed at the upper limit of *Larix*) to a maximum of 100 percent on the 810-m site (watershed ridge) and a minimal 8 percent on the 1,030-m site (weakly wind protected and too cold for insects ecotope).

Confirmation of the negligible character and amount of insect damage is also seen in the level of seed extraction

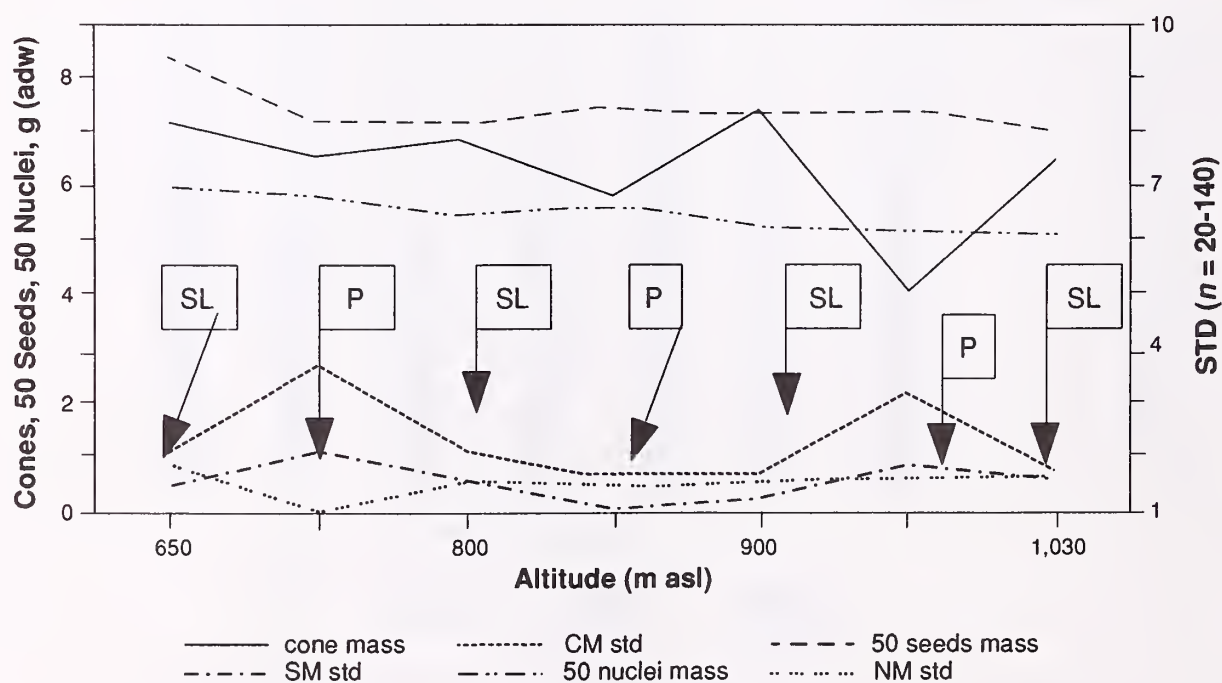


Figure 7—Variations in *Pinus pumila* cones, seeds, and nuclei mass. SL—slopes, P—Plateau.

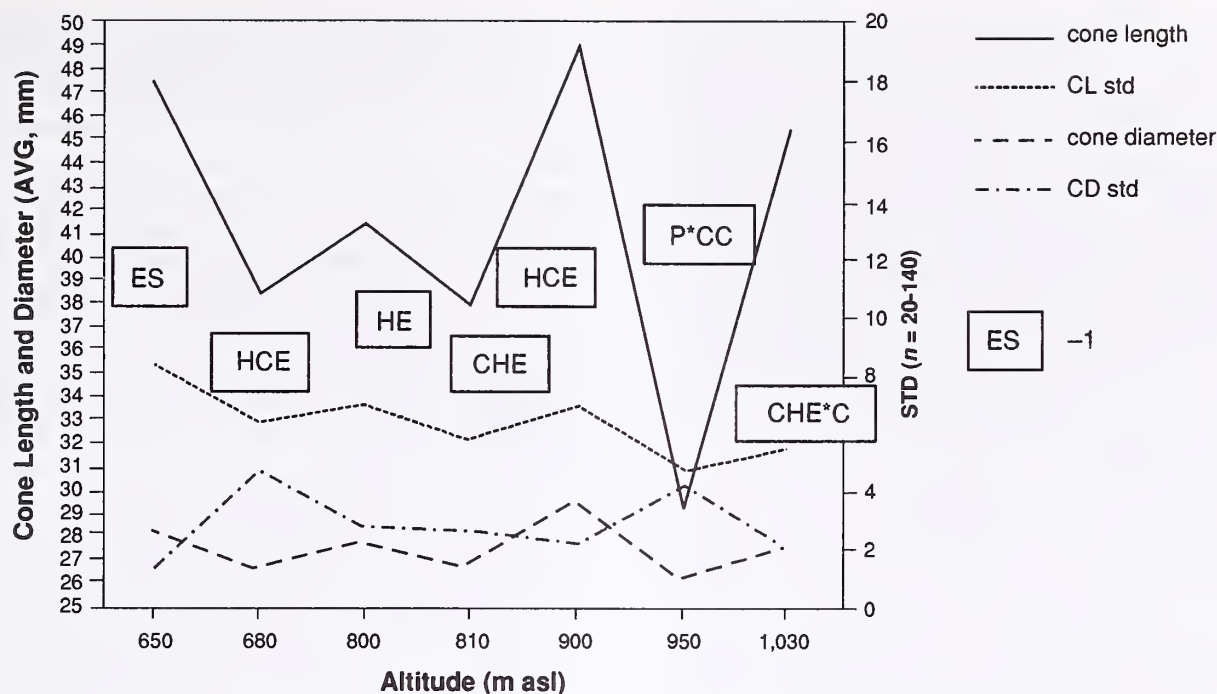


Figure 8—Variations in *Pinus pumila* cone size. 1—forest type (see table 1).

by the nutcracker, which collects only full, matured seeds (fig. 9).

DISCUSSION AND CONCLUSIONS

Data analysis results, combined with some previous material, allow us to make some conclusions about *Pinus pumila* seed production in Kamtchatka, keeping in mind the fragmentary nature of our study, even though it was done in typical environmental conditions.

1. The main conclusion is that *P. pumila* seed production has such a high potential in time and space that we can speak about the environmental (abiotic and natural biotic) impact on it in the frame of modification only but not in the frame of regulation. Environmental stresses usually cannot cause a crop crisis—trees have compensating mechanisms both at the organismic and population

level, and one of them is the microhabitat mosaics of annual seed production.

2. *Pinus pumila* seed production is not (in Kamtchatka, at least) significantly dependent on altitude and site conditions. Landscape conditions (above facial level) are the most important. However, this is true only when trees are not overshadowed by neighboring upright trees; that is, when Pp forms an independent vegetational belt in more or less solid segments—in plain or mountain tundra, upper forest-tundra ecotone, on the seashore dunes, in wide river valleys, etc. Pp often grows as the lower canopy of more or less dense *Larix* forests (more than 30 percent of *Larix* cover), which have the same age and the same syngenetic origin (very often in pyrogenetic ecotopes). These shaded dwarf pine usually do not produce seeds and develop vegetatively only.

3. The utmost upper limits of distribution (1,300-1,400 m above sea level) are unfavorable for Pp seed production,

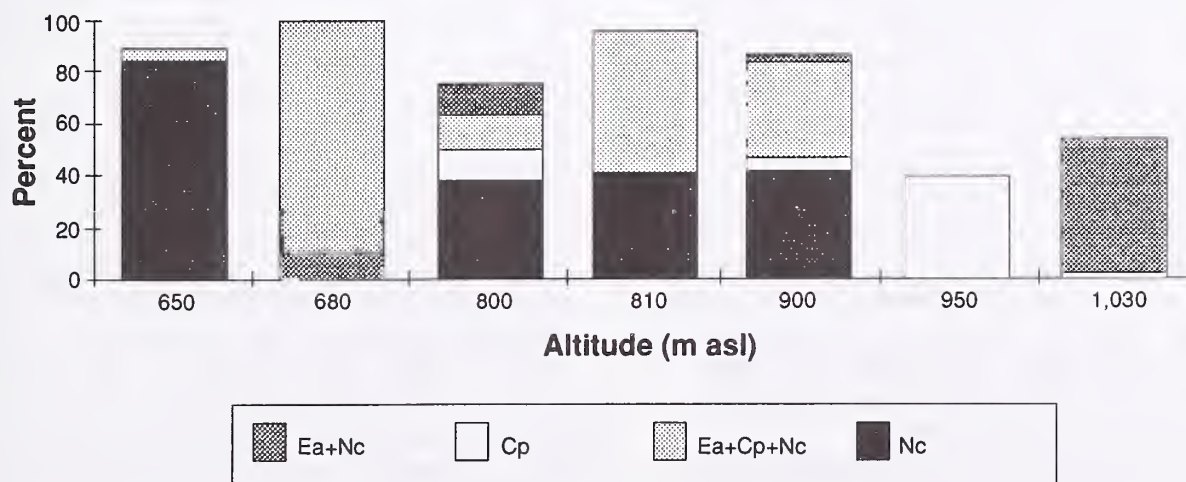


Figure 9—Percentage of cones damaged by insects and birds. Cp—*Cecidomyia pumila*; Ea—*Eupithecia abietaria*; Nc—*Nucifraga caryocatactes*.

mainly because of low temperature and phenological delay. But even here, some cones can be found, and sometimes the crop can be abundant in wind-protected habitats. Phenological delay often prevents the nutcracker from collecting seeds here. These seeds, having been dispersed by birds from lower sites, and having more stable genotypes, provide a better chance for successful reforestation in new areas. At the same time, dwarf pine regeneration at high altitudes is more or less provided by the remaining abundant seeds. Besides this, numerous zooconsorts (mainly micromammals) will have a good food supply most valuable in extreme conditions.

The same unfavorable conditions for seed production can be found in the Pp belt at the seashore (Pacific Kamtchatka coast), on the dunes nearest to the water. But here, as well as in the mountains, trees utilize each opportunity for maximal realization of their reproduction ability. Pp seed production on the second to third dune of the coast belt is equal in cone size and mass parameters to those at the 900- to 1,000-m altitude and in seed and nuclei parameters to those at the 650- to 750-m altitude in the continental climate portion of the peninsula.

Conditions moderately favorable for Pp seed production can be found in plain and submountain (foothill) places, for instance on gravel-sandy fluvioglacial or proluvial deposits, where abundant cone crops sporadically occur.

The most productive seed zone lies in the vegetation belt within the 600-900 m above sea level area. Here, cone crops are mostly permanent and stable from year to year.

4. Successful seed production of Pp needs the following conditions: in winter—sufficient snow cover to protect buds of low-lying trees from freezing; in summer—high insolation, good wind protection on cold sites, absence of shading, and good drainage for the root systems. The main adaptive feature of Pp is its ability to lay close to the ground in the autumn. This process is initiated by low temperature in the autumn before the snow cover. This unique feature provides good chances of survival under very extreme conditions. Strict dependence of Pp on snow cover depth is proved by coincidence of its area border with the snow depth isoline of 40 cm and more (Lukitcheva 1964; Tstcherbakova 1964).

5. Special research and preliminary work, including mapping of various productivity sites, is needed for the practical (silvicultural) estimation of current or future cone crops of Pp. It is possible to show, as an example, the scope of crop diversity. In the middle elevation site (700-800 m), with 5 g of seed mass in the cone, 80 percent of germinating shoots, and 80 percent of Pp covering the ground, we can get about 110 kg of seeds per hectare. At the upper limit of seed production, with 2 g of seed mass in the cone, 30 percent of germinating shoots, 10 percent of covering, we can get about 1 kg of seeds per hectare. High variability of cone crop is illustrated in table 1 data: taking into account only pure stands of Pp (without considering its real distribution on the surface) we can see that the crop size on the 650-m site is about 6.5 kg/ha, and about 212 kg/ha on the 950-m site.

6. Starting from the elevation that corresponds to the upper limit of upright trees distribution (900 to 1,000 m)

in Kamtchatka, Pp produces an increasing number of shoots. This can be interpreted as a organismic compensation for the increasing severity of abiotic environmental conditions. Photosynthetic ability increases, seed production potential, as we saw, remains at the same high level, and seed protection (thickness of seed walls) becomes stronger. All this takes place mostly in the subalpine belt and proves Pp belongs mainly to this type of vegetation. Coincidence of these activated processes with the upper limit of upright trees distribution allows us to hypothesize the existence of some kind of temperature threshold-trigger. It could be the sum of effective temperatures, above which the development of upright tree forms is possible, and below which only prostrate forms develop.

7. We agree with the opinion that Pp, as well as other stone pines, has a high evolutionary potential, revealing itself in prominent and wide polymorphism of reproductive organs and their functional flexibility (Pravdin and Iroshnikov 1982). This is well illustrated by our work and other sources. Ecotypical features are also evident, accompanied by stability of the main seed-production parameters. In fact almost all of this is similar to that which is known from other Pp regions (Bobrinev and Rylkov 1984; Efremova and Ivliev 1972; Kapper 1954; Khomentovsky and Khomentovskaya 1990; Krylov and others 1983; Rush 1974).

8. Pp seed production potential exceeds the possibilities of its realization in our research area, and most likely, in the Kamtchatka peninsula as a whole. Ecotopical diversity in Kamtchatka is evidently only a part of the whole scope of acceptable conditions for the species (here we can admit that low temperatures affect vegetative growth three to four times more than they affect generative organs variability). Therefore, we should look for possible phylogenetic roots of this species in the regions with a wider geoeological spectrum of sites.

9. Our observations (partly presented in this paper) allow us to speculate that Pp is a middle-altitudinal species, with more preferable growth conditions in the moderately continental climate (in relatively humid mountains) than at the seashore. But, regarding the whole area, the definite and necessary influence of Pacific wet air masses results in considerable snow cover.

Combining this conclusion with some known hypotheses of Pp evolution (Sotchava and Lukitcheva 1953; Tikhomirov 1949; etc.) we think that this dwarf tree species most likely appeared in Tertiary times in some climatically subcontinental mountain regions of Angarida (northeastern Asia). In Kamtchatka, pollen data show Pp has been here for 1-1.5 million years (Malaeva 1967; Tchelebaeva and others 1974). During Pleistocene interglacial periods, and in the early middle Holocene, Pp occupied periglacial zones and other places unacceptable for more-thermophil tree species. The highest incidence of polyembryony and underdevelopment of seeds in Kamtchatka support the possible centers of origin in the moderate continental climates when compared to Magadan (northeastern continental part of Asia) and Buryatia (southern part of eastern Siberia) (Iroshnikov 1972; Rush 1974). These features can be considered a reaction to less favorable conditions of the secondary environments,

including Kamtchatka peninsula. According to A. I. Iroshnikov (1972), Pp is one of the most well-adapted species to the continental climate of northeastern Asia.

REFERENCES

- Bobrinev, V. P.; Rylkov, V. F. 1984. Seed production of dwarf stone pine. Inform. bull. of Tchitinsky Information Center, #76-84. Tchita. 5 p. [In Russian].
- Efremova, L. S.; Ivliev, L. A. 1972. On dwarf stone pine seed producing at Kamtchatka. In: Utilization and reproducing of forest resources in the Far East. Abstr. of the all-union conference Khabarovsk. Part 2: 158-159. [In Russian].
- Iroshnikov, A. I. 1972. Seed producing and seed quality of conifers in northern and mountainous regions of Siberia. In: Seed producing of Siberian conifers (collection of papers). Novosibirsk: 98-117. [In Russian].
- Kapper, O. A. 1954. Conifers (forestry characteristics). Moscow-Leningrad. 304 p. [In Russian].
- Khomentovsky, P. A.; Efremova, L. S. 1991. Seed production and cone-feeding insects of *Pinus pumila* at Kamtchatka peninsula: aspects of coexistence. In: Baranchikov, Y. N.; Mattson, W. J.; Hain, F. P.; Payne, T. L., eds. Forest insects guilds: patterns of interaction with host trees. U.S. Department of Agriculture, Forest Service, Gen. Tech. Rep. NE-153: 316-320.
- Khomentovsky, P. A.; Kazakov, N. V.; Tchernyagina, O. A. 1989. Tundra-forest zone at Kamtchatka: problems of conservation and management. In: Problems of nature management in taiga zone (collection of papers). Irkutsk: 30-46. [In Russian].
- Khomentovsky, P. A.; Khomentovskaya, I. G. 1990. Geographical variability of *Pinus pumila* seed producing at Kamchatka. In: Questions of Kamchatka geography. Petropavlovsk-Kamchatsky. No. 10: 47-55. [In Russian].
- Krylov, G. V.; Talantsev, N. K.; Kozakova, N. F. 1983. Siberian pine (*Pinus sibirica* Du Tour). Moscow. 216 p. [In Russian].
- Kunitsin, L. F. 1963. A pattern of Kamtchatka nature regionalization. In: Nature conditions and regionalization of Kamtchatka district. Moscow: 7-26. [In Russian].
- Lukitcheva, A. N. 1964. Distribution areas of Asia plants (a map). In: World geographical atlas. Moscow. 112 p.
- Malaeva, E. M. 1967. Kamtchatka vegetation development in Pliocene-Pleistocene. In: Development of Siberian and far-eastern vegetation in Quaternary (collection of papers). Moscow: 78-170. [In Russian].
- Pravdin, L. F.; Iroshnikov, A. I. 1982. Genetics of *Pinus sibirica* Du Tour, *P. koraiensis* Sieb. et Zucc. and *P. pumila* Regel. Annales Forestales. 9(3): 79-123.
- Rush, V. A. 1974. Biochemical characteristics of five-needle pines seeds. In: Biology of conifer seed reproduction in western Siberia (collection of papers). Novosibirsk: 180-184. [In Russian].
- Sokolov, I. A. 1973. Volcanism and soils formation (with Kamtchatka as an example). Moscow. 224 p. [In Russian].
- Sotchava, V. B.; Lukitcheva, A. N. 1953. On geography of dwarf stone pine. Reports of the USSR Academy of Sciences. 90(6): 1163-1166. [In Russian].
- Tchelebaeva, A. I.; Shantser, A. E.; Egorova, I. A.; Lupikina, E. G. 1974. Cenozoic deposits of the Kuril-Kamtchatka area. In: Kamtchatka, Kuril and Commander islands (series of History of the relief development.) Moscow: 31-57. [In Russian].
- Tikhomirov, B. A. 1949. Dwarf stone pine (*Pinus pumila* (Pall.) Rgl), its biology and utilization. MOIP series, botan. division, Moscow. 14(6): 106 p. [In Russian].
- Tstcherbakova, E. J. 1964. An average of maximal decade snow depths (a map). In: World geographical atlas. Moscow. 220 p.

NEEDLE LONGEVITY AND PHOTOSYNTHETIC PERFORMANCE IN CEMBRAN PINE AND NORWAY SPRUCE GROWING ON THE NORTH- AND EAST-FACING SLOPES AT THE TIMBERLINE OF STILLBERG IN THE SWISS ALPS

Takayoshi Koike
Rudolf Häsler
Hans Item

Abstract—The number of shoots in each age class and the photosynthesis of the shoots were measured on cembran pine (*Pinus cembra*) and Norway spruce (*Picea abies*) growing on north- and east-facing slopes at 2,185 m above sea level. Needle longevity on the north-facing slope exceeded needle longevity on the east-facing slope by 1 to 3 years in both species. A negative correlation between maximum photosynthesis and needle lifespan was found. However, there was no physiological difference in the photosynthesis of trees on the respective slopes.

In the Swiss Alps, cembran pine (*Pinus cembra*) grows around timberline level and Norway spruce (*Picea abies*) from valleys to mountainsides (Kuoeh and Amiet 1970). At the subalpine timberline, the growth and biomass increase of trees are strongly influenced by the microsite performance and microclimate (Livingston and Black 1987; Schönenberger and Frey 1988; Turner and others 1982). Using the monitoring experiment on photosynthetic production as a basis, the biomass increase of mountain pine (*Pinus mugo*) growing at the timberline was found to be regulated by the soil temperature and the net radiation (Häsler 1982). However, physiological characteristics of trees were not revealed. Is the turnover rate of needles related to the tree size? What about the physiological adaption of needles to the microclimate?

In this study, these questions, needle lifespan and the age-related photosynthesis of cembran pine planted on north- and east-facing slopes, were measured. We present the physiological parameters of needle photosynthesis. Anatomical traits of needles were investigated with reference to the estimation of the intercellular CO₂ concentrations (C_i) (Terashima 1992). We discuss the trade-off relation between the needle lifespan and photosynthetic rates influenced by the microclimate.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Takayoshi Koike, Rudolf Häsler, and Hans Item are members of the "Ecophysiology" group, Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland. Present address of T. Koike: Forest Products Research Institute, Sapporo 062, Japan.

MATERIALS AND METHODS

At the study site (Stillberg in the Swiss Alps), on the north-facing slope, the yearly net radiation surplus was 308 kWh/m² lower, and the root-zone temperature during growth period was 2-4 °C lower than on the east-facing slope at 2,185 m above sea level (a.s.l.) (Turner and others 1982). The mean soil temperature at 10 cm on the north- and east-facing slopes from June to September was 3.5 and 4.5 °C, respectively (Koike and others, submitted).

Plant Materials

Plants studied were cembran pine, (provenance 2,050 m a.s.l.) and Norway spruce (provenance 1,960 m a.s.l.), raised from seeds in the nursery at Birmensdorf ZH (550 m a.s.l.). The cembran pines were transplanted in 1975, and the Norway spruces in 1962, to the experimental site (2,185 m a.s.l.). Mean tree height as of 1988 on the north-facing slope and east-facing slope was 40 cm and 80 cm in cembran pine and 36 cm and 45 cm in Norway spruce, respectively. For measurements of photosynthesis, attached shoots within the even-aged needles were used. Younger shoots were removed when the photosynthesis of older shoots was measured. The cut shoot ends were sealed with vaseline.

Measurements

The gas exchange rate was measured with a thermoelectrically controlled chamber (Mini-cuvette Walz, FRG), which was coated with aluminium foil in order to fully use diffuse light (Koike and others, submitted). Photosynthesis was determined with two infrared gas analyzers (Binos, Leybold-Heraeus, FRG). Dew point mirrors (Walz, FRG) were used to measure the absolute air humidity. Needle temperatures were monitored by a 0.1 mm chromel-constantan thermocouple. The PPFD above the needles was measured with a GaAsp photodiode (Hamamatsu G1118, J) after calibration with a LiCor quantum sensor (USA). A CO₂ dispensing apparatus (Walz, FRG) produced different CO₂ concentrations in the chamber.

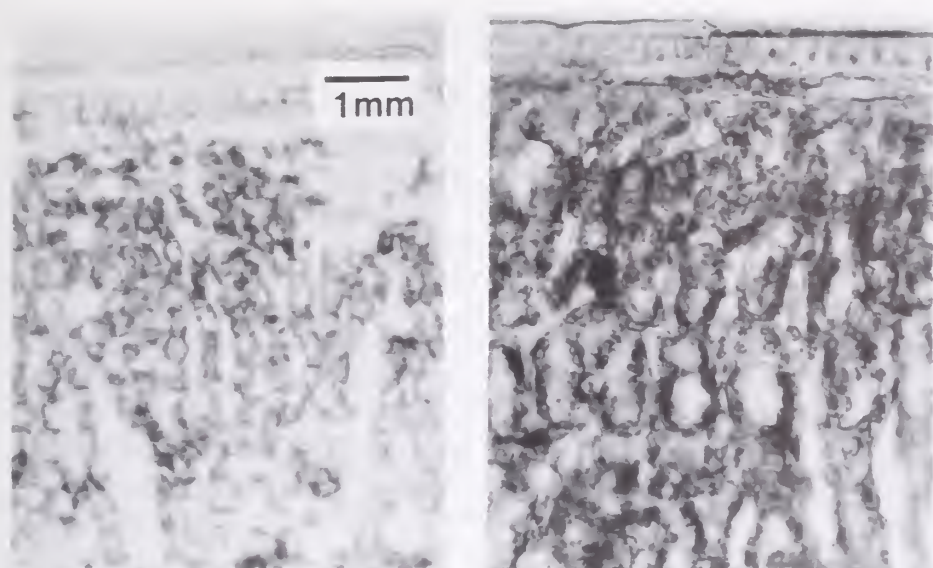


Figure 1—Cross section of a needle of a cembran pine (right) and a Norway spruce (left).

Anatomy of needles was observed with a microscope after needles were sectioned with a microtome (Leitz). Total needle surface area of the used twig was estimated by the modified glass bead method (Davies and Benecke 1980). The number of specimens for the census of needle longevity was more than 700 shoots of 10 trees. Dry weight of the needles was determined after 48 hours drying at 80 °C. Nitrogen concentration in the needles was analyzed with a CHN analyzer (Rapid, USA).

RESULTS

Needle Characteristics

The anatomy of needles of cembran pine and Norway spruce was similar to the "homobaric" leaves (fig. 1). There was no extension of vascular bundle sheaths into the mesophyll. Needle lifespans of cembran pine and Norway spruce were 9 and 12 years for the north-facing slope and 8 and 9 years for the east-facing slope, respectively (fig. 2). The proportion of older needles of both species was larger on the north-facing slope than on the east-facing slope. In Norway spruce, the frequency of younger needles on the north-facing slope was smaller than that on the east-facing slope. A negative correlation between the light-saturated photosynthesis and needle longevity was found in both species (fig. 3).

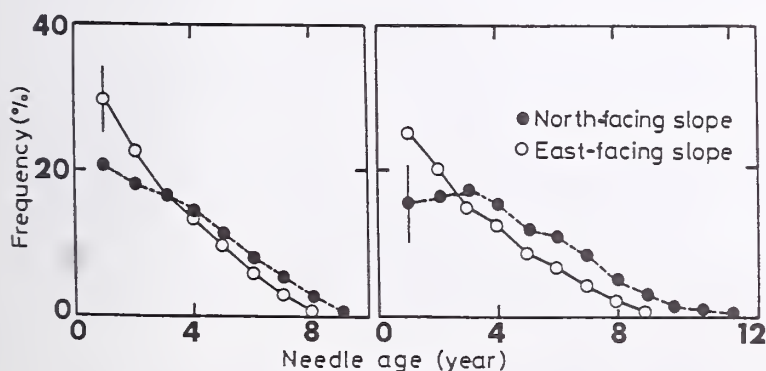


Figure 2—Frequency of needle age in percent of total needles of cembran pines (right) and Norway spruces (left) growing on east-facing and north-facing slopes at timberline.

Physiological Parameters

There was a positive correlation between the stomatal conductance and the light-saturated photosynthesis in both species (fig. 4). No difference between the north- and east-facing slopes was found. The quantum yield and carboxylation efficiency (CE) of both species on the north-facing slope tended to be lower than of those on the east-facing slope (table 1).

The maximum photosynthesis at light and CO₂ saturation (P_{max}) of both species on the north-facing slope was lower than that on the east-facing slope ($P < 0.05$). The CE of cembran pine was slightly higher than that of Norway spruce. The nitrogen concentration in needles of cembran pine was higher than in needles of Norway spruce. However, there was no statistical difference in both species between the slopes.

DISCUSSION

The estimation of C_i is based on the uniform response of the stomata of a leaf (Terashima 1992). The anatomy of needles of cembran pine and Norway spruce was similar to the homobaric leaf. Non-uniform stomatal aperture in needles of loblolly pine was observed only when needles

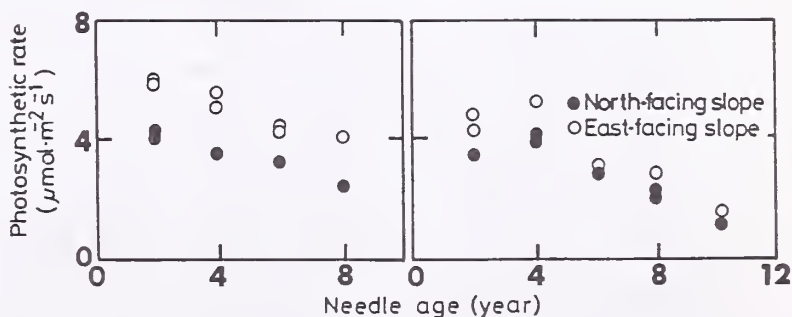


Figure 3—Photosynthesis in relation to needle age in cembran pines (left) and Norway spruces (right) growing on east-facing and north-facing slopes at timberline.

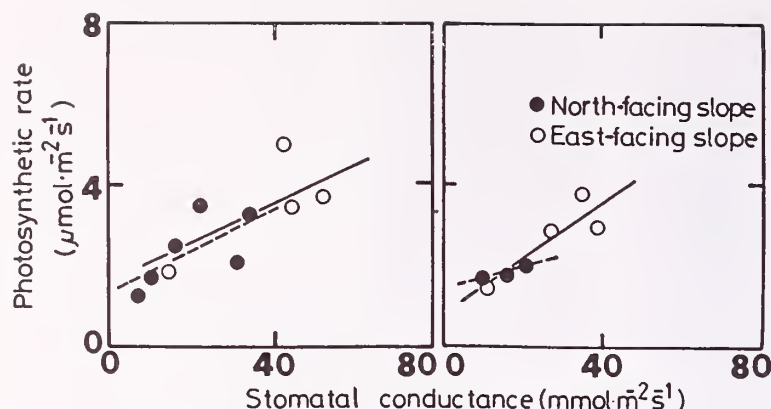


Figure 4—Photosynthesis in relation to stomatal conductance in cembra pines (left) and Norway spruces (right) growing on east-facing and north-facing slopes at timberline.

were treated with abscisic acid, not with the low temperature in roots (Day and others 1991). According to these facts, we can estimate the CE calculated with C_i values.

The P_{max} from needles of the north-facing slope was smaller than of those of the east-facing slope, while needle lifespan of the north-facing slope increased. Many physiological parameters in needles from the north-facing slope were almost the same as those on the east-facing slope. However, slightly lower P_{max} in both species from the north-facing slope may be attributed to the lower soil temperature (Day and others 1991; Häsler 1982, Turner and others 1982). The lower P_{max} of needles from the north-facing slope may be compensated for by the longer lifespan of needles. Tree growth on the north-facing slope may be retarded by the shortage of radiation and low soil temperatures.

ACKNOWLEDGMENTS

We thank Dr. H. Turner for providing the climate data of the Stillberg site, Prof. W. K. Smith for collecting references, and Mrs. M. J. Sieber for editing the English version of this manuscript.

REFERENCES

- Davies, C. E.; Benecke, U. 1980. Fluidized bed coating of conifer needles with glass beads for determination of leaf surface area. *Forest Science*. 26(1): 29-32.
- Day, T. A.; Heckathorn, S. A.; DeLucia, E. H. 1991. Limitations of photosynthesis in *Pinus taeda* L. (loblolly pine) at low soil temperatures. *Plant Physiology*. 96: 1246-1254.
- Häsler, R. 1982. Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. *Oecologia*. 54: 14-22.
- Koike, T.; Häsler, R.; Matyssek, R.; Item, H. Seasonal changes in the photosynthetic capacity of *Larix decidua* and *Pinus cembra* planted on contrasting slopes at the timberline at Stillberg (Davos), eastern Switzerland. *Trees*, submitted.
- Kuoch, R.; Amiet, R. 1970. Die Verjüngung im Bereich der oberen Waldgrenze der Alpen. Eidgenössische Anstalt für das forstliche Versuchswesen, Mitteilungen. 46: 159-328.
- Livingston, N. J.; Black, T. A. 1987. Stomatal characteristics and transpiration of three species of conifer seedlings planted on a high elevation south-facing clear-cut. *Canadian Journal of Forest Research*. 17: 1273-1282.
- Schönenberger, W.; Frey, W. 1988. Untersuchungen zur Ökologie und Technik der Hochlagenaufforstung. Forschungsergebnisse aus dem Lawinenanrissgebiet Stillberg. *Schweizerische Zeitschrift für Forstwesen*. 139: 735-820.
- Terashima, I. 1992. Anatomy of non-uniform leaf photosynthesis. *Photosynthesis Research*. 31(3): 195-212.
- Turner, H.; Häsler, R.; Schönenberger, W. 1982. Contrasting microenvironments and their effects on carbon uptake and allocation by young conifers near alpine tree-line in Switzerland. In: Waring, R. H.: Carbon uptake and allocation in subalpine ecosystems as a key to management: Proceedings of the IUFRO Workshop, P1.07-00, Corvallis, OR: Oregon State University: 22-30.

Table 1—Physiological parameters of cembra pine and Norway spruce growing on an east- and a north-facing slope of an avalanche gully at Stillberg (2,185 m a.s.l.)

Parameter	Cembra pine			Norway spruce		
	E slope	N slope		E slope	N slope	
Quantum yield (mol CO ₂ •mol/quanta)	0.014 ± 0.004	0.009 ± 0.002	ns	0.012 ± 0.006	0.006 ± 0.002	ns
Carboxylation efficiency (μmol•m ⁻² •μbar ⁻¹)	0.024 ± 0.009	0.022 ± 0.009	ns	0.017 ± 0.002	0.018 ± 0.008	ns
P_{max} (mol•m ⁻² •s ⁻¹)	8.30 ± 1.51	5.38 ± 0.77	(¹)	6.87 ± 1.61	4.93 ± 0.12	(¹)
Nitrogen concentration (mg•g ⁻¹)	12.26 ± 0.90	13.27 ± 0.91	ns	10.43 ± 1.87	9.26 ± 1.22	ns

¹P < 0.05.

THE BROAD-LEAVED KOREAN PINE FOREST IN CHINA

Luo Ju Chun

Abstract—Korean pine (*Pinus koraiensis*) is a tree species of high economic value. Its natural distribution area, the characteristics of distribution in the broad-leaved Korean pine forest region of China, the biological and ecological characteristics of Korean pine, the forest types of Korean pine, and the succession pattern of the Korean pine forest communities have been studied. The results are significant to conservation and sustaining use of Korean pine.

Korean pine (*Pinus koraiensis*) is well known for its high-quality timber that can be used for many different purposes. Undoubtedly, Korean pine is one of the most important tree species in Chinese forests.

Except for a few pure Korean pine forests, the species often occurs in the "conifer-broad-leaved tree mixed-forest communities" with many species of deciduous broad-leaved trees and other conifers, which is the most representative vegetation formation in the northeastern humid zone in China.

NATURAL DISTRIBUTION AREA

Korean pine—a relict species from the Tertiary—mainly occurs in northeast Asia and in a narrow zone along the west coast of the Japan Sea. This zone includes the southern part of eastern Russia, the eastern part of northeast China, North Korea, and the center of Honshu in Japan. The main natural range of Korean pine, however, is in China. Korean pine is a representative species in Dahurian flora, and also is the main forest tree species in the eastern mountains of northeast China.

In China, the broad-leaved Korean pine forest is found from 40°15' N. to 50°20' N. and from 126° E. to 135° E., east of Song-nen plain and north of Song-liao plain. In the south it reaches Dan dong, in the north Hei-Ho county. The whole area takes a crescent shape covering Lesser Xingan Ling, Wan Da Mountain, Zhang Guang Cai Ling, Lao Ye Ling, and Chang Bai Mountain. Most of these mountains are trending from northeast to southwest. They are characterized by gentle topography and low elevation, not higher than 1,300 m. There are many different tree species, including many quite valuable broad-leaved trees. Their exploitation began more than 100 years ago. Their timber output still makes up one-fourth of total timber production in China.

The forest region, which is influenced by the Japan Sea, is characterized by temperate-zone monsoon climate. The

warm and moist climate is favorable to growth of Korean pine. Annual average temperature is 0-6 °C; the growing season is about 4-5 months. Temperature sum (≥ 10 °C) is about 2,500-3,200 °C. At higher latitude, temperature is low, winter is long, and summer short. Winter covers 5 months. January is the coldest month; the absolute minimum temperature is -40 to -30 °C. In July, which is the warmest month, mean temperature reaches 20-24 °C. Winter is characterized by thick snow cover and mean temperatures ranging from -28 to -14 °C. Annual precipitation amounts to 600-1,100 mm and decreases from south to north; maximum is in summer (June to August). The annual relative humidity is about 60-70 percent. Humidity and temperature are favorable to growth of Korean pine and other trees.

The soil in Korean pine forests is dark brown forest soil with a thick humus layer, and it is very fertile.

CHARACTERISTICS OF VEGETATION DISTRIBUTION

Horizontal Distribution

Because of the wide range of Korean pine forest, the climate is quite different from north to south in the distribution area. Consequently, some differences in flora and plant communities become apparent. The distribution area can be divided into two subzones: northern and southern temperate. The demarcation is from Don-g Nin in the eastern part of Jing Bo Lake to Ji Lin district until its west boundary; it seems to run along the parallel of 44 °N. The differences in natural conditions and vegetation can be described as follows:

1. In the northern subzone, climate is cold, the growing season is only about 100-120 days, and annual rainfall amounts to 500-700 mm; the southern subzone is characterized by a warm and humid climate and a growing season of 130-150 days. Annual precipitation is about 700-1,100 mm.

2. In the northern subzone, more conifers typical of the cold-temperate zone (for example, *Picea koraiensis*, *P. jezoensis*, and *Abies nephrolepis*) occur in Korean pine forests. *Pinus pumila* can be found in the subalpine. In addition, *Quercus mongolica* is more common on exposures to sun. *Larix gmelinii* forests, mixed with *Betula platyphylla*, occur in the lowlands. *Vaccinium vitis-idaea*, *Ledum palustre*, *Vaccinium uliginosum*, *Betula fruticosa*—representatives of Dahurian flora—are typical of larch forest undergrowth. In the southern subzone, there are more representatives of Chang Bai flora, such as *Picea jezoensis* var. *komarovii*, *Abies holophylla*, and *Larix olgensis*.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Luo Ju Chun is Professor of Ecology and Forest Management, Forestry Resource College, Forestry University, Beijing, China.

3. In the southern subzone there are more plant species than in the north. The forest often consists of 30-40 woody species forming three layers. In the southern subzone there are twice as many broad-leaved tree species in Korean pine forests than in the northern subzone; the genus *Acer*, for instance, is represented by only five species in the north, compared to 12 species in the south. The percentage of valuable broad-leaved trees (such as *Fraxinus mandshurica*, *Juglans mandshurica*, *Phellodendron amurense*, *Tilia amurensis*, *Ulmus propinqua*) in Korean pine forests is higher in the southern than in the northern subzone. These broad-leaved trees usually grow together with *Betula costata* and *Acer mono* and represent more than 50 percent of the species of southern Korean pine forests. Moreover, *Carpinus cordata* and *Fraxinus rhynchophylla* are very common in the south, but occur rarely in the north. In addition, there are more than 10 vine plant species in the southern subzone, but only five or six in the north.

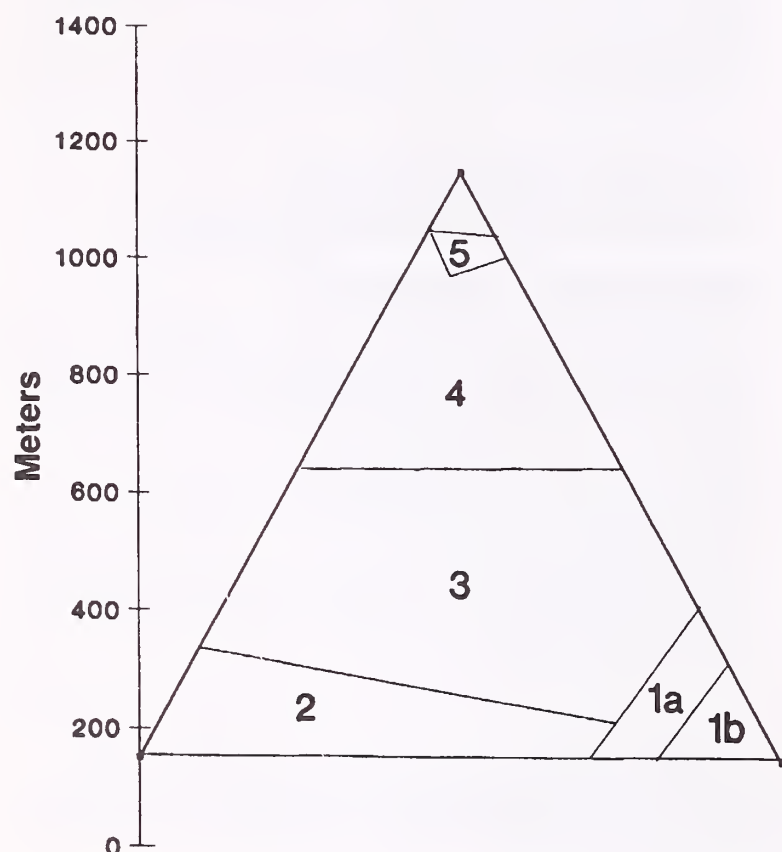


Figure 1—Vertical distribution pattern of vegetation in Lesser Xin An Ling (southern exposures): 1a, River head-valley-conifer forest with larch, spruce, fir; 1b, Bank depression, broad-leaved forest with *Ulmus propinqua*, *Fraxinus mandshurica*, *Phellodendron amurense*; 2, Oak forest (*Quercus mongolica*) mixed with *Betula dahurica*, *Tilia mandshurica*; 3, Broad-leaved Korean pine forest mixed with spruce, fir, *Betula costata*, *Tilia amurensis*, *Ulmus laciniata*; 4, Spruce-fir forest belt; 5, Subalpine *Betula ermanii*-*Pinus pumila* elfin forest belt.

Vertical Distribution

The vertical distribution pattern of vegetation in Lesser Xin An Ling (fig. 1) is a typical example of the northern subzone:

1. River valley forest: It is composed of *Picea jezoensis*, *Abies nephrolepis*, *Larix gmelinii*, *Juglans mandshurica*, *Ulmus propinqua*, *Populus ussuriensis*, and other species.

2. Oak (*Quercus mongolica*) broad-leaved forest belt (150-300 m): It is secondary forest that established after destruction of virgin conifer-broad-leaved mixed forest, and it occurs usually on shallow soils on sun-exposed slopes.

3. Broad-leaved Korean pine forest belt (250-650 m): Korean pine is the dominant species; spruces and firs occasionally occur; the broad-leaved trees make up less than 30 percent of the species. The volume of standing timber is the highest (300-600 m³/ha) in the northern forest region. Korean pine grows on exposures to south and south-west, on mountain ridges, and on hill tops.

4. Spruce-fir forest belt (650-1,000 m): *Picea koraiensis*, *Picea jezoensis*, and *Abies nephrolepis* are the main tree species.

5. Subalpine moss-elfin forest belt (1,000-1,080 m): The climate is cold and humid; wind is strong. The elfin forest is composed of *Betula ermanii*. This species exhibits dwarf growth forms not taller than 4-6 m. *Pinus pumila* grows in the forest understory. The forest floor is covered mainly by moss.

The vertical distribution pattern of vegetation in the southern subzone can be illustrated by the situation of Chang Bai Mountain (fig. 2):

1. Broad-leaved forest belt (250-500 m a.s.l.): It is formed by *Quercus mongolica*, *Betula platyphylla*, *Betula dahurica*, and *Populus davidiana*. It is a typical secondary forest following destruction of broad-leaved Korean pine forest. Locally, basswood, maple, elm, walnut, and corktree form mixed forests. At lower elevations, these broad-leaved forests are scattered.

2. Broad-leaved Korean pine forest belt (500-1,200 m): Korean pine is the main species, and is mixed with various broad-leaved trees: *Betula costata*, *Carpinus costata*, *Ulmus laciniata*, *Acer mono*, *Tilia amurensis*, *Quercus mongolica*, especially the valuable broad-leaved tree species *Ulmus propinqua*, *Phellodendron amurense*, *Juglans mandshurica*, *Fraxinus mandshurica*, and, at valley bottoms, some spruce and fir can be found.

3. Spruce-fir forest belt (1,200-1,800 m): It is formed by *Picea jezoensis*, *Picea koraiensis*, and *Abies nephrolepis*, with additional *Betula ermanii* and *Larix olgensis* in the upper part of the belt, or with Korean pine, *Betula costata*, *Ulmus laciniata*, and *Tilia amurensis* in its lower part.

4. Subalpine *Betula ermanii* mossy elfin forest belt and subalpine meadow belt (1,800-2,100 m): These belts are characterized by cold and windy climate, steep topography, and shallow soils. *Betula ermanii* forests alternate with vast meadow areas.

5. Alpine tundra belt (>2,100 m): Vegetation consists of different dwarf shrub species, mosses, and lichens.

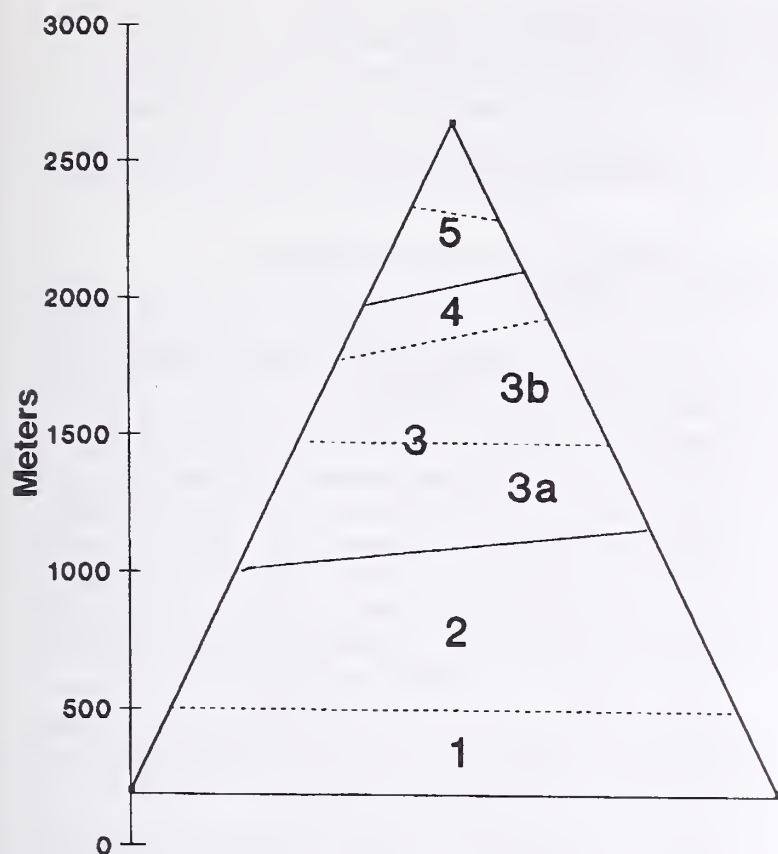


Figure 2—Vertical zonal spectrum of vegetation in Chang Bai Mountain: 1, Secondary deciduous broad-leaved forest; 2, Conifer-broad-leaved mixed forest (broad-leaved Korean pine forest); 3, Coniferous forest belt: 3a, Spruce-fir-Korean pine forest subbelt; 3b, Spruce-fir coniferous forest subbelt; 4, Subalpine *Betula ermanii*-elfin forest belt, and subalpine meadow belt; 5, Alpine tundra belt.

As far as we know, the higher the latitude the lower is the upper limit of Korean pine. In the southern subzone Korean pine occurs up to 1,200 m a.s.l.; in the north its uppermost altitudinal limit is located at about 650 m.

BIOLOGICAL AND ECOLOGICAL CHARACTERISTICS

Korean pine is a long-lived species. Its lifespan is 300-400 years, sometimes 500 years. Tree height usually reaches 30 m. The diameter can reach 1 m. Korean pine is one of the valuable sawtimber trees in the world. It grows slowly in the first 5-8 years. After the age of 10 its growth rate increases rapidly. Its diameter growth begins to accelerate at the age of 12. The height growth becomes more rapid after 16-18 years. Accelerated growth continues until the age of 30. Korean pine is a tree species growing fastest at middle age. In general, growth rate of Korean pine increases earlier in plantations than in natural forests. In clear cuttings, the radial growth of 8-year-old trees is 2.6 times higher than in natural forests, and height growth is twice as much as in trees at the same age that became naturally established.

Secondary growth of Korean pine is common in autumn, but it appears mainly in trees less than 10 years old. After 80 years growth, Korean pine reaches a height of 18-20 m. At this age the tree top often begins to fork and bear cones. Obviously, the forking is closely related to cone production.

Korean pine has shallow roots. Its taproot is underdeveloped and degenerates easily. Thus, seed trees left on clear cuttings are sensitive to windbreak.

Most Korean pine trees begin to produce cones at the age of 80-100 years. Nevertheless, cones can also be found on 30-year-old trees. In plantations, however, even 20-year-old trees are able to bear cones.

There are two ecotypes of Korean pine: one is the leptodermis form displaying thin bark with small and shallow scale or long strip lobes. It forks less, grows faster in height, and produces better timber. The other is the pachidermis form characterized by deep and large, long, square-shape lobes on the tree trunk. It forks more, grows slower in height, and the timber quality is not as good as in the leptodermis type. The leptodermis type should be used for afforestation.

Korean pine belongs to thermophile species; its vegetative growth requires 6-7 °C of the lowest average temperature and the most suitable temperature is 14-16 °C in the young stage. The relative moisture it demands is 70 percent and, during the period of most rapid growing, relative humidity of about 70 percent is required. Korean pine is intolerant to high temperature during vegetative growth. If average temperature exceeds 15-16 °C, height growth will decrease or even stop. On the other hand, it will not be affected by winter temperatures as low as -50 °C.

At seedling stage a little shading is favorable to Korean pine, although it can tolerate full sunlight. Its light requirement increases with age. While 3 years old, seedlings require 60-70 percent of incoming solar radiation. After the fifth year, young trees become totally shade intolerant.

Korean pine grows best on thick, moist, fertile, and well-drained soils with pH 5-6, but it can also exist on shallow dry soil, poor in nutrients. It grows badly on soils rich in clay. However, Korean pine requires appropriate soil moisture. In bogs and on sites with stagnant water, growth is hampered, and Korean pine is rarely seen there.

PRINCIPAL FOREST TYPES

Mu Dan Jiang forest region, the distributive center of Korean pine, may serve as an example to classify Korean pine forest into the following forest types:

Steep-Slope *Carex calltnichos*-Korean Pine Forest—This type occurs on sunny exposures or narrow ridges at an altitude of 800-1,000 m. These usually are poor sites. The community can be divided into two layers. The forest canopy is formed by Korean pine (90 percent) and *Quercus mongolica* or *Tilia amurensis* (10 percent), which have a higher crown density than Korean pine. In the second layer there is some Korean pine, spruce, fir, and linden. The growing stock is 400-500 m³/ha. The dominant species on the forest floor are *Carex calltnichos* and *C. ussuriensis*.

Corylus-Carex-Korean Pine Forest—This type is found on mountains with gentle slopes at altitudes of 700-900 m. As to favorability to tree growth, these sites can be considered intermediate. Korean pine prevails (60-70 percent) followed by *Tilia amurensis* (20 percent), and some *Abies nephrolepis*, *Picea jezoensis*, *Ulmus propinqua*, *Acer mono*, and *Betula costata*. The growing stock is about 400-500 m³/ha. There are more tree species associated, such as *Acer* sp. There is more undergrowth, and the main species is *Corylus mandshurica*. On the forest floor about 30 species are to be found. *Carex siderosticta* and ferns are the most common plants.

Fern-Spruce-Fir-Korean Pine Forest—This type occurs on the lower gentle slopes (inclination about 10°) of the mountains or along side streams at an altitude of 500-800 m. The community construction is complex. The canopy layer is formed by Korean pine and some *Populus ussuriensis* and *Picea jezoensis*. The second layer is composed of *Picea jezoensis* and *P. koraiensis* (50 percent), *Abies nephrolepis* (20 percent), and *Tilia amurensis* (20 percent). Other species are *Betula costata*, *Ulmus laciniata*, *Acer mono*, *Phellodendron amurense*, *Juglans mandshurica*, *Fraxinus mandshurica*, and many kinds of maple. Because of better site conditions, growing stock is higher (250-350 m³/ha for the first story and 200 m³/ha for the second story). The undergrowth is abundant with over 20 species; about 30 species occur on the forest floor. Ferns are dominant (such as *Dryopteris*).

Fern-Moss Korean Pine Forest—This type is found in the lower part of mountains or in broad valleys; slope inclination is 0-5°. Two stories can clearly be distinguished: *Pinus koraiensis* (80 percent) and a few *Picea jezoensis*, *Fraxinus mandshurica*, *Ulmus propinqua*, *Acer mono*, and *Tilia amurensis* form the forest canopy. In the second story there is more *Picea jezoensis*, *Betula costata*, *Acer mono*, *Abies nephrolepis*, *Tilia amurensis*, and a few *Juglans mandshurica*, *Fraxinus mandshurica*, *Ulmus propinqua*, *Betula platyphylla*, and many kinds of maple.

So the tree species are very abundant. This forest type is typical of the sites most favorable to tree growth. The growing stock can reach 600 m³/ha. The undergrowth mainly consists of *Lonicera* sp., *Viburnum* sp., and *Sorbaria*, and is well developed. *Carex* and multiple fern and luxuriant moss cover are common throughout the area.

COMMUNITY SUCCESSION PATTERNS

Two succession patterns for the broad-leaved Korean pine communities are obvious:

Succession Without Disturbance—Natural regeneration is poor under virgin Korean pine forest cover, although a comparatively large quantity of seedlings may appear after a seed year. However, they will only be able to grow up if the canopy is cut thin. Because Korean pine lives longer than other coniferous and broad-leaved trees, and tolerates shade for longer period, it tends to form multigeneration and multistoried forests.

Succession After Disturbance—After destruction of broad-leaved Korean pine forest the succession goes on as shown by the following sequences:

Selective cutting → conifer-broad-leaved mixed forest in which main elements are broad-leaved trees. Protection → broadleaved-Korean pine forest.

Clear cutting or fire → secondary bare land. Protection → grass and shrub communities → conifer-hardwood mixed forests in which main elements are hardwood trees → conifer-broad-leaved mixed forest in which main elements are coniferous trees → broad-leaved-Korean pine forest.

To promote the reestablishment of Korean pine forest, management should be adjusted to this succession process.

CLIMATES WHERE STONE PINES GROW, A COMPARISON

Tad Weaver

Abstract—While stone pine climates are similar, species adapted to relatively moderate climates may be excluded from the ranges of congeners by more severe climates, and species with longer warm-moist growing seasons are probably more productive than congeners. Absolute low/summer average/absolute high temperatures for stone pines listed in order of increasing absolute low temperature are *Pinus sibirica* (−55/13/37 °C), *P. pumila* (−52/9/36 °C), *P. koraiensis* (−42/11/36 °C), *P. albicaulis* (−34/9/29 °C), and *P. cembra* (−23/8/27 °C). The Walter drought index shows little stress in stone pine forests despite large differences in summer/winter precipitation: in order of increasing summer rainfall, precipitation is *P. albicaulis* (102/829mm), *P. pumila* (142/264mm), *P. sibirica* (187/245mm), *P. cembra* (323/616mm), *P. koraiensis* (394/242mm). Estimated thawed-soil growing season increases from *P. albicaulis* (4.5mo), through *P. pumila* (4.6mo), *P. sibirica* (5.5mo), and *P. cembra* (6.3mo) to *P. koraiensis* (7.8mo); growing seasons of the first three trees could be shortened by drought.

Stone pines grow in most of the boreal zone (fig.1) (Fullard and Darby 1964; Lanner 1990; Mirov 1967). *Pinus pumila* and *P. sibirica* occupy vast far-northern (50 to 70° N. latitude) areas in northeastern Asia; *P. sibirica* ranges from just west of the Urals (55° E. longitude) halfway to the Pacific (115° E. longitude) and *P. pumila* ranges from 115° E. longitude to the Pacific (165° E. longitude). *P. koraiensis* grows at the boreal-deciduous forest transition in eastern China (120 to 150° E. longitude and 45 to 55° N. latitude with outliers to 35° N. latitude at high altitude). Paralleling *P. koraiensis*, *P. albicaulis* occupies the Rocky-Cascade-Sierra Mountain chains of North America from 55° N. latitude southward to 45° N. latitude with outliers to near 35° N. latitude. *Pinus cembra* appears in the Alps at approximately 45° N. latitude. Glaciated parts of the conifer forest zone—both in northern Europe and North America—lack stone pines (fig.1).

Due to their common ancestry and common boreal forest habitat, one expects the trees to occupy similar climates. This paper tests that hypothesis by comparing climates occupied by the trees with respect to 20 factors that may be important in determining the ranges and productivities of the species. The information may be especially useful for predicting the success of introductions—from one region to another—of stone pines, their tree associates,

and to some degree, even their herb, cryptogam, and animal associates. Such introductions might be of interest as either producers or pests.

METHODS

Climates of environments dominated by closely related stone pines (Lanner 1990; Mirov 1967) were compared. The comparisons are nonstatistical, since the objective was to discuss biological responses rather than the climates themselves.

The climates were characterized by choosing three to four stone pine stands at which temperature and precipitation were regularly measured (a complete sample of accessible data); summarizing the data for periods of 10 years (*P. albicaulis* and *P. cembra*) or longer (unspecified); and calculating means for selected parameters. The stations studied are listed here—from west to east—each with its approximate latitude, longitude, and altitude (m). Note that *P. albicaulis* and *P. cembra* grow significantly higher than, and to the south of, the Asian pines. Asterisked Siberian stations lack most temperature data. Scientists who helped identify weather stations in stone pine climates are listed in the acknowledgments.

Pinus albicaulis stations (USDC 1961-80) were Crater Lake, OR (43° N., 122° W., 1,990m), Ellery Lake, CA (38° N., 119° W., 2,940m), Old Glory, BC (49° N., 119° W., 1,008m), and Kings Hill, MT (46° N., 110° W., 2,225m). *Pinus cembra* stations (contributed by W. Tranquillini) were Haggen (47° N., 11° E., 1,800m), Obergurgl (47° N., 11° E., 2,070m), and Patscherkofel (48° N., 11° E., 1,952m). *Pinus sibirica* stations (Muller 1982) were Serov (60° N., 61° E., 132m*), Surgut (61° N., 73° E., 40m), Kolpasevo (58° N., 83° E., 76m*), Jenisejsk (58° N., 92° E., 78m*), Krasnojarsk (56° N., 93° E., 15m), Tura (64° N., 100° E., 130m*), Irkutsk (52° N., 104° E., 468m), and Kirensk (58° N., 108° E., 256m). *Pinus pumila* stations (Muller 1982) were Vitujsk (64° N., 122° E., 107m*), Jakutsk (62° N., 130° E., 100m*), Verchojansk (68° N., 133° E., 137 m), Ochotsk (59° N., 143° E., 6 m), Zyranka (65° N., 151° E., 43m*), Petropavlovsk-Kamchatskij (53° N., 159° E., 32m), Apuka (65° N., 170° W., 10m*), and Anadyr (65° N., 178° E., 62m). *Pinus koraiensis* stations (contributed by Luo Ju Chun and Zhao Shidong) were AnTu (43° N., 128° E., 591m), Chagbei-ShenYang (42° N., 128° E., 738m) and YiChun (48° N., 129° E., 231m).

Parameters studied describe climates with respect to temperature, precipitation, and growing season. The following three paragraphs list these parameters and outline the rationales for their choice; the rationales are developed further in Weaver (1993) and in the following discussion.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Tad Weaver is Plant Ecologist, Biology Department, Montana State University, Bozeman, MT 59717.

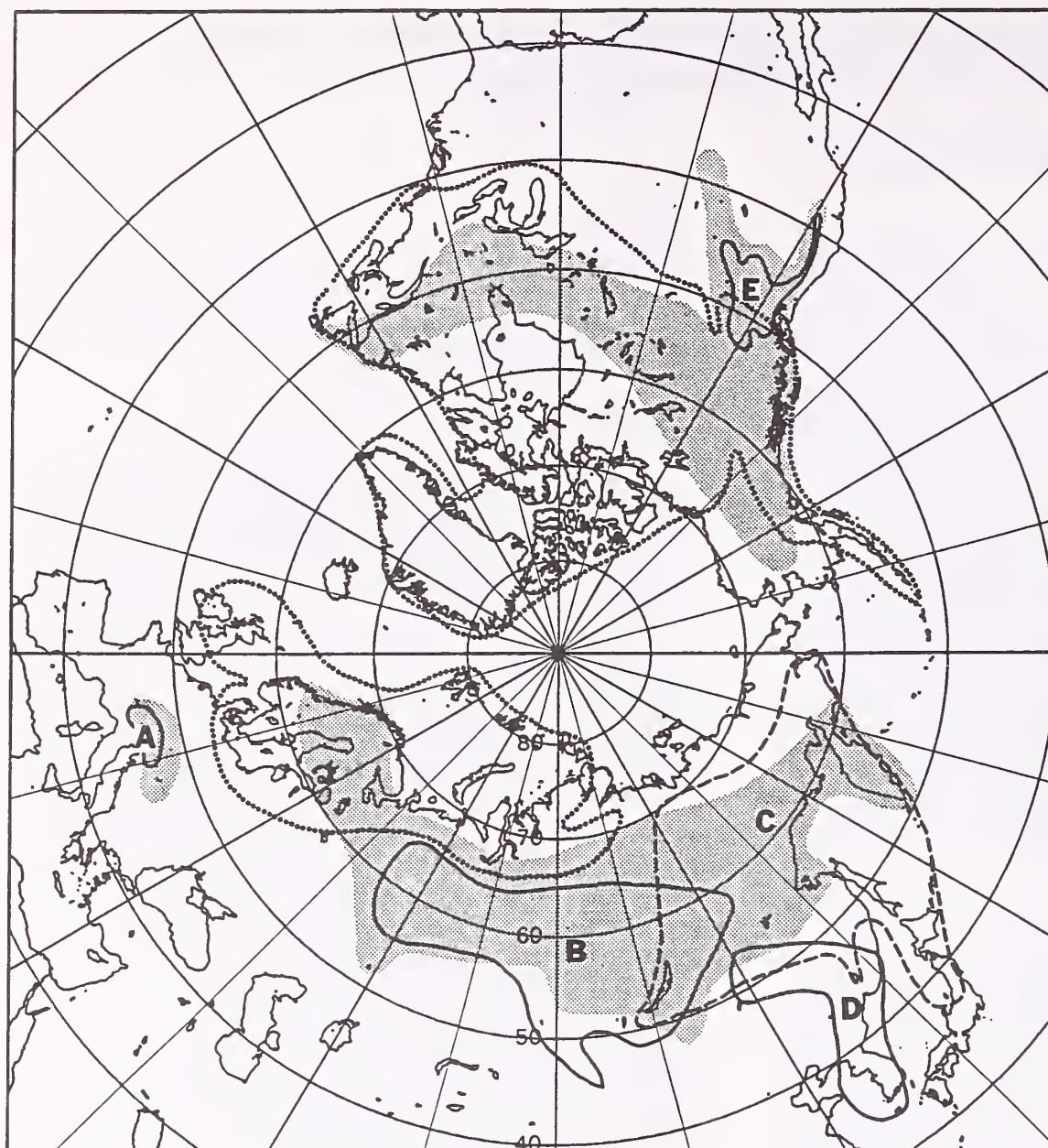


Figure 1—Distribution of stone pines in relation to space, conifer forests, and pleistocene glaciation. North America and Eurasia are seen from a polar view. Shading locates the conifer zone on the two continents (Fullard and Darby 1964). Areas within the dotted lines received pleistocene glaciation (Denton and Hughes 1981). Ranges of the stone pines (Mirov 1967) are outlined by solid or dashed lines: A = *Pinus cembra*, B = *P. sibirica*, C = *P. pumila*, D = *P. koraiensis*, E = *P. albicaulis*. The absence of stone pines in the conifer zone of northwestern Eurasia and parts of North America could be due to glaciation.

Ten temperature parameters were compared. Midwinter frost danger was described by the long-term minimum temperature (the absolute low), the average January minimum, and the average January maximum. Extreme fall and spring frosts are represented by the absolute low in the first and last months of winter (that is, the absolute lows in the months with 0°C average air temperature; Weaver 1994). The average growing-season temperature was calculated across those months when average air temperatures were above 0 °C. This average was recalculated using “temperature growth support units = Q” to account for the rise in rates of metabolic processes with rising temperature; these points lie on a curve defined by 0 °C = 0, 1 °C = 1, 11 °C = 2, 21 °C = 3, 31 °C = 4, and 41 °C = 5 (Weaver 1994). Summer highs were represented by the average July minimum, average July maximum, and long-term high.

Seven precipitation parameters were compared. October-June precipitation was measured to determine whether soil was moist in winter and at the opening of

the growing season. Summer precipitation was indexed by July-September precipitation and by precipitation in the wettest and driest month in that period. Since plants require water, not precipitation, months with a positive water balance were estimated with the Walter index (Nielson 1986; Walter 1973), which assumes that for every 2 °C rise in average temperature 1 mm of precipitation will be evapotranspired. Two derivatives were studied: drought months (duration of periods with a negative water balance) and drought magnitude (total estimated deficit). While the Walter index tends to underestimate drought (Stephenson 1990), it may be adequate in these cool climates. Poikilohydric (Larcher 1975) organisms may be more dependent on a number of growing hours set by the number of rain days than on total precipitation; rain days per month were therefore recorded.

Four growing-season parameters were compared. Length of the growing season was indexed first as the number of months when air temperature is above 0 °C, that is, the approximate number of months when the soil is thawed

(Weaver 1994). Second, drought months (none according to the Walter index) were subtracted from the warm-season index to create a better warm-moist season index. Despite contrary observations (Weaver 1994), growth is expected to be indexed by the integral of temperature over growing season. Thus two indices of growing season productivity (Weaver 1994) were calculated: [growing season \times (average growing season temperature -5°C) (Chang 1968)] and, considering the Q_{10} effect, [growing season \times average growing season Q].

WINTER TEMPERATURES

Average winter (January) temperatures in northeastern Asia are the world's coldest and they warm southward (Fullard and Darby 1964). Normal daily lows in regions occupied by the trees are *Pinus pumila* (-30°C), *P. sibirica* (-27°C), *P. koraiensis* (-27°C), *P. albicaulis* (-14°C), and *P. cembra* (-8°C), respectively (table 1). Daily highs in winter average 8°C higher (table 1).

Absolute lows experienced by *Pinus sibirica* (-55°C) and *P. pumila* (-52°C) rise to *P. koraiensis* (-42°C), *P. albicaulis* (-34°C), and *P. cembra* (-23°C) (table 1). *Pinus albicaulis* and *P. cembra* may be protected from extreme low temperatures by the drainage of cold air from their mountaintop sites. Becwar and Burke 1982 show that timberline conifers of the Colorado Rockies do not survive temperatures below -40°C ; thus *P. sibirica* and *P. pumila* may be the only stone pines tolerant of -50°C .

Frosts of early fall and late spring may catch trees in partially hardened states. Absolute lows in the first and last months of winter were -21°C for *P. koraiensis*, -17°C for *P. sibirica*, and -10°C for the remaining trees. Why are absolute lows for fall-winter-spring frosts lower in the *P. koraiensis* and *P. sibirica* regions than in the *P. pumila* regions where average temperatures are lower (table 1; Fullard and Darby 1964)?

SUMMER TEMPERATURES

Continentality allows northeastern Asia to warm in summer more than less continental parts of the polar region. Thus absolute maximum temperatures of *Pinus sibirica* (37°C) and *P. pumila* (33°C) are considerably higher than those of *P. cembra* (27°C) and *P. albicaulis* (29°C) (table 1). Absolute summer highs in the *P. koraiensis* forest at the boreal-deciduous forest transition are as high (36°C) as in interior forests. Average July highs in *P. sibirica* and *P. koraiensis* forests are like those in Rocky Mountain Douglas-fir (*Pseudotsuga menziesii*) forests, a vegetation zone below the Rocky Mountain stone pine zone (Weaver 1994).

Daily growth rates are determined by average temperature conditions in the growing season. (1) Temperature conditions are represented most simply by average temperature; this is 13°C for *Pinus sibirica*, 11°C for *P. koraiensis*, and 8 to 9°C for *P. pumila*, *P. albicaulis*, and *P. cembra*. Like July highs, 13°C average temperatures, are similar to those found in the Douglas-fir/ponderosa pine forests of the Rocky Mountains (Weaver 1994). (2) Because growth rises exponentially with increasing temperature (Q_{10} ; Larcher 1975), a better index of temperature on growth may be a cross-season average of growth support units (Weaver 1994), which give greater weight to high than low temperatures. With this index climates cool from *P. sibirica* to *P. albicaulis* to *P. pumila*-*P. koraiensis* to *P. cembra* (table 1).

PRECIPITATION

Winter-spring precipitation is high in *Pinus albicaulis* (829 mm) and *P. cembra* (616 mm) and lower (about 250 mm) in northeastern Asia (table 2). Since the lower amounts will saturate most mountain soils (Weaver 1978), the excess is expected to run off, to have little effect on water supplies in forest stands during the growing season,

Table 1—Temperatures¹ in stone pine communities of the world. Climates are listed in order of increasing winter temperatures

Temperature data	Species, location, number of stations ²				
	<i>P. pumila</i> N. China 4+	<i>P. sibirica</i> Siberia 4+	<i>P. koraiensis</i> Korea-China 3	<i>P. albicaulis</i> N. America 4	<i>P. cembra</i> Euro-Alps 3
Winter Temperature					
Jan. mean min	-30.0 ± 8.0	-27.0 ± 2.0	-27.0 ± 2.0	-14.0 ± 2.0	-8.0 ± 0.0
Jan. mean max	-24.0 ± 9.0	-19.0 ± 2.0	-11.0 ± 2.0	-5.0 ± 3.0	-1.0 ± 1.0
Abs min	-52.0 ± 4.0	-55.0 ± 2.0	-42.0 ± 1.0	-34.0 ± 2.0	-23.0 ± 1.0
Frost spring	-11.0 ± 3.0	-18.0 ± 2.0	-26.4 ± 0.2	-11.0 ± 1.0	-10.0 ± 1.0
Frost fall	-11.0 ± 3.0	-16.0 ± 2.0	-27.6 ± 0.7	-11.0 ± 1.0	-10.0 ± 1.0
Summer Temperature					
July mean min	8.0 ± 0.0	12.0 ± 1.0	14.0 ± 1.0	4.0 ± 1.0	5.0 ± 1.0
July mean max	15.0 ± 2.0	21.0 ± 1.0	26.0 ± 0.0	18.0 ± 1.0	14.0 ± 1.0
Abs max	33.0 ± 1.0	37.0 ± 1.0	36.0 ± 2.0	29.0 ± 1.0	27.0 ± 2.0
T_{gs}	9.0 ± 1.0	13.0 ± 1.0	11.3 ± 1.2	9.0 ± 1.0	8.0 ± 1.0
Q_{gs}	1.9 ± 0.2	2.4 ± 0.1	1.9 ± 0.1	2.1 ± 0.2	1.7 ± 0.1

¹Temperature data ($^{\circ}\text{C}$) are the mean \pm one standard error. Absolute temperatures are recorded for 10 years in *P. albicaulis* and *P. cembra*; records for the Asian pines are unspecified (presumed longer). T_{gs} and Q_{gs} are growing season averages defined in the text.

²Sample size is four for *P. albicaulis* (except average max and min for January and July, $n = 5$), three for *P. cembra*, and for both *P. pumila* and *P. sibirica* eight, except for January max-min, July max-min, and spring-fall frost temperatures where $n = 4$.

and, thus, to have little effect on production. Large snowfalls in the *P. albicaulis* and *P. cembra* forests, relative to those in the Asian forests, surely result in greater snowpacks, which shelter ground-level plants and animals less frost tolerant than the trees.

Summer precipitation is lower where moisture carrying air masses cross mountains (northeastern Asia and the Rocky Mountains) than where they do not (Alps and eastern China). Thus summer rainfall increases from *Pinus albicaulis* (102 mm) to *P. pumila* (187 mm), *P. sibirica* (187 mm), *P. cembra* (323 mm), and *P. koraiensis* (394 mm). Precipitation in the driest month parallels summer rainfall (table 2).

Soil water may be adequate in spite of low rainfall if evapotranspiration is low. If we assume that 1 °C degree evaporates 2 mm per month (Nielson 1986, 1992; Walter 1973), we see that stone pines do not experience drought in any month (table 2). In addition, some buffering against drought occurs because snowmelt water stored in the soil provides a supplement to summer showers. However, even at boreal temperatures Walter's index may understate evaporation (Stephenson 1990), so there is probably less summertime restriction of growth by drought (stomate closure) in *Pinus cembra* and *P. koraiensis* than in *P. albicaulis*, *P. sibirica*, and *P. pumila* forests.

Organisms without water reserves—such as lichens, mosses, and invertebrates—are more sensitive to summer drought and may distinguish wetter and drier forests. These organisms are surely inhibited in *Pinus pumila* and *P. albicaulis* forests (one to eight rain days/month) relative to *P. cembra* and *P. koraiensis* forests (16 to 18 rain days).

GROWING SEASON

Survival depends on photosynthetic provisioning for winter respiration and the outcome of competition may depend on excesses above this basic provisioning. One expects production to be correlated with the number of warm-moist days, with the warmth of those days (Q_{10} , Larcher 1975), and thus with their product.

If water stress never occurs, the length of the warm-moist season increases from *Pinus albicaulis* (4.5 mo) to *P. pumila* (4.6 mo), *P. sibirica* (5.5 mo), *P. cembra* (6.3 mo), and *P. koraiensis* (7.8 mo) (table 3). And if temperature conditions were identical in these forests, one would therefore expect production in *P. cembra* and *P. koraiensis* forests to be half again as great as in *P. pumila* and *P. albicaulis* forests. Actual differences could be even larger because the temperature-defined growing season may overstate stand productivity in drier regions. For example, while subsoils remain moist all summer in higher (J. Brown, personal communication) and lower (Weaver 1974) parts of the *P. albicaulis* zone, drying of surface soils apparently causes tree water stress at lower (B. Keane, personal communication), but not higher (J. Brown, personal communication), sites. Similar droughty periods probably occur in warmer *P. pumila* and *P. sibirica* forests.

Production is expected to rise exponentially with rising temperature, and thus productivity might be better correlated with the product of season length and temperature "growth supporting units." While this production hypothesis was rejected in a cross-vegetation zone analysis (Weaver 1994), the genetic similarity of stone pines might allow it to operate here. If so, and if water deficits in Siberia do not shorten the growing season, *P. koraiensis* and *P. sibirica* will be promoted to the most productive stone pines (table 3).

CONCLUSIONS

From a tree's point of view, average conditions in the stone pine zones are similar: water stress is slight or nonexistent and growing season temperatures average 9 to 13 °C. Seasonal extreme conditions may, however, prevent reciprocal transplantation. Winter or fall-spring frosts in the *Pinus sibirica*/*P. pumila*/*P. koraiensis* region may exclude the other pines. And weak droughts in the *P. albicaulis*/*P. pumila*/*P. sibirica* regions might exclude *P. cembra* or *P. koraiensis*.

Table 2—Precipitation¹ in stone pine forests of the world. Climates are listed in order of increasing summer precipitation

Precipitation data	Species, location, number of stations ²				
	<i>P. albicaulis</i>	<i>P. pumila</i>	<i>P. sibirica</i>	<i>P. cembra</i>	<i>P. koraiensis</i>
	N. America 4	N. China 4+	Siberia 4+	Euro-Alps 3	Korea-China 3
Total	931 ± 229	407 ± 137	432 ± 21	939 ± 9	636 ± 68
Oct.-June	829 ± 234	264 ± 76	245 ± 22	616 ± 43	242 ± 62
July-Sept.	102 ± 14	143 ± 43	187 ± 11	323 ± 36	394 ± 17
Wettest summer month	116 ± 16	165 ± 25	181 ± 8	214 ± 15	346
Driest summer month	4 ± 4	4 ± 2	8 ± 2	45 ± 16	32
Summer drought months	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Summer water deficit	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Summer rain days, average number	8 ± 1	1 ± 1	14 ± 1	16 ± 1	18

¹Precipitation (mm) data are total (sum of all months), winter, summer (July, August, plus September), driest summer month (July-September) recorded, wettest summer month (July-September) recorded, and average number of showers in June-September. High variances in total precipitation for *P. albicaulis* and *P. pumila* are reduced to 705 ± 51 mm and 274 ± 37 mm by omission of the Crater Lake and Petropavlovsk stations, respectively.

²Sample size is four for *P. albicaulis*, three for *P. cembra*, three for *P. koraiensis*, and eight for both *P. pumila* and *P. sibirica*, except for summer drought months and deficit, where it is only four.

Table 3—Stone pine productivity correlates: growing season,¹ growing season temperature,² and their products. Climates are listed in descending order by one estimate of productivity, warm moist season

	Species, location, number of stations				
	<i>P. koraiensis</i> Korea-China 2	<i>P. cembra</i> Euro-Alps 3	<i>P. sibirica</i> Siberia 4	<i>P. pumila</i> N. China 4	<i>P. albicaulis</i> N. America 4
Warm season	7.8 ± 0.1	6.3 ± 0.2	5.5 ± 0.2	4.6 ± 0.4	4.5 ± 0.3
Summer drought months	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Warm-moist season	7.8 ± 0.1	6.3 ± 0.2	5.5 ± 0.2	4.6 ± 0.5	4.5 ± 0.3
T _{gs}	11.3 ± 1.2	8.0 ± 1.0	13.0 ± 1.0	9.0 ± 1.0	9.0 ± 1.0
Q _{gs}	1.9 ± 0.1	1.7 ± 0.1	2.4 ± 0.1	1.9 ± 0.2	2.1 ± 0.2
GS × T _{gs} -5 °C	56.5	18.9	44.0	18.4	18.0
GS × Q _{gs}	15.6	10.7	13.2	8.7	9.5

¹Warm-season and warm-moist season are two indices of growing season. Warm-season months occur after average monthly air temperature rises above 0 °C and before it falls below 0 °C. The warm-moist season is the warm season minus any months in which T/2 is greater than P(mm), Walter 1973; "Walter drought" does not occur in stone pine regions.

²Two indices of growing-season temperature are provided. T_{gs} is the average temperature in growing season months. T_{gs}-5C is used as one index of growth support on the assumption that growth does not occur below 5 °C (Chang 1968). Q_{gs} is the average of temperatures weighted for their growth-supporting capacity: 0 °C = 0, 1 °C = 1, 11 °C = 2, 21 °C = 4 (Weaver 1993).

Organisms filling other niches might find the climates dissimilar (Weaver 1990). Poikilohydric organisms and humans would react differently to the relatively summer-rainy climates of the *P. cembra* and *P. koraiensis* regions than to the other stone pine climates. And organisms wintering under snow—small mammals, insects, plants of small stature—are more protected from the extremes of winter cold in the *P. cembra* and *P. albicaulis* regions than in the other climates.

ACKNOWLEDGMENTS

I thank (1) W. Tranquillini (University of Innsbruck, Austria) for providing data from his *P. cembra* weather stations, (2) J. Luo (Beijing Forestry University, China) and Z. Shidong (Inst. Appl. Ecol., Shenyang, China) for providing data from weather stations in *P. koraiensis* climates, (3) H. Lieth (University of Osabuck, Germany), P. Gorchakovsky (Acad. Sci. Inst. Ecol., Ekaterinburg, Russia) and P. Khomentovsky (Kamchatka Inst. Ecol., Petropavlovsk, Russia) for help in selecting *P. sibirica* and *P. pumila* weather stations, and (4) nineteen North American ecologists already acknowledged (Weaver 1990) for help in selecting North American *P. albicaulis* stations. I am also grateful for support to the project provided through Intermountain Research Station contract #INT-92720-RJVA (W. Schmidt).

REFERENCES

- Becwar, M.; Burke, M. 1982. Winter hardiness limitations and physiography of woody timberline flora. In: Li, P.; Sakai, A. Plant cold hardiness and freezing stress. New York: Academic Press: 307-324.
- Chang, J. 1968. Climate and agriculture. Chicago: Aldine. 304 p.
- Fullard, H.; Darby, H. 1964. The university atlas. London: George Philip and Son. 176 p.
- Lanner, R. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt, W.; McDonald, K., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 72-79.
- Weaver, T. 1994. Vegetation distribution and production in Rocky Mountain climates—with emphasis on whitebark pine [these proceedings].
- whitebark pine ecosystems: ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.
- Larcher, W. 1975. Physiological plant ecology. New York: Springer. 252 p.
- Mirov, N. 1967. The genus *Pinus*. New York: Ronald Press. 602 p.
- Muller, M. 1982. Selected climatic data for a global set of standard stations for vegetation science. The Hague, Netherlands: Junk. 306 p.
- Neilson, R. 1986. High resolution climatic analysis and southwest biogeography. Science. 232: 27-33.
- Nielson, R. 1992. Toward a rule based biome model. Landscape Ecology. 7: 27-43.
- Stephenson, N. 1990. Climatic control of vegetation distribution: the role of water balance. American Naturalist. 135: 649-670.
- Walter, H. 1973. Vegetation of the earth in relation to climate and ecophysiological conditions. New York: Springer. 237 p.
- Weaver, T. 1974. Root distribution and soil water regimes in nine habitat types of the northern Rocky Mountains. In: Marshall, J., ed. The belowground ecosystem. Sci. Ser. 26. Fort Collins, CO: Colorado State University, Range Science Department. 351 p.
- Weaver, T. 1979. Changes in soils along a vegetational (altitudinal) gradient of the northern Rocky Mountains. In: Youngberg, C., ed. Proceedings of the Fifth North American forest soils conference. Madison, WI: Soil Science Society America. 14-29.
- Weaver, T. 1990. Climates of subalpine pine woodlands. In: Schmidt, W.; McDonald, K., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 72-79.

Growth Characteristics



International Workshop
St. Moritz 1992

GROWTH OF SWISS STONE PINES THAT ORIGINATED FROM AND WERE PLANTED AT SEVERAL ALTITUDES IN THE AUSTRIAN ALPS

Kurt Holzer

Abstract—For the purpose of gene conservation, a plus tree collection of Swiss stone pine (*Pinus cembra*) was conducted. Scions of 185 trees and 82 open-pollinated seed samples were collected within the natural range of Swiss stone pine in Austria. In 1987, clonal height was measured at an age between 25 and 30 years. Open-pollinated families were planted at three different sites. Height was measured after 18 years. Growth of graftings and open-pollinated families helped identify the altitude of their origin. When planted below timberline, growth decreased with increasing altitude.

In 1957, the Department of Forest Tree Breeding and Genetics, Federal Forestry Research Institute, Austria, commenced a selection program of Swiss stone pine (*Pinus cembra*). The objectives of this program were to preserve genetic resources of superior trees in a clonal orchard and to assess the growth capacity of the clones by field performance of open-pollinated families.

Within the natural range of stone pine, timberline divides the distribution of stone pine, due to environmental conditions, into two silvicultural zones: (1) production forests and (2) "Kampfzone." Hence, those aspects had to be considered for the program (Holzer 1963, 1976).

MATERIAL AND METHODS

Covering the majority of natural stands in Austria, 185 superior trees were selected between 1958 and 1965 (Holzer 1961, 1969). Within production forests scions of 124 and above timberline ("Kampfzone") scions of 61 individuals were collected. The altitudinal range was approximately 250 m below and 230 m above timberline (between 1,650 m and 2,200 m above sea level). In addition, open-pollinated seeds were harvested from 82 trees.

Graftings were planted in a conservation orchard in Purkersdorf-Stadlhütte near Vienna at 400 m above sea level. Progenies were raised in the nursery of the institute (Mariabrunn Vienna, 220 m above sea level) for 6 to 8 years and then planted at three different sites: (1) Purkersdorf-Stadlhütte; (2) Große Zirbenwiese (1,650 m above sea level); Seetaler Alpen, a swampy meadow within the natural range of stone pine, approximately

250 m below timberline; and (3) Melcheben, Packalpe (1,700 m above sea level), close to timberline of Norway spruce (*Picea abies*). At sites 2 and 3, only 32 families were planted because of limited numbers of plants.

In 1987, height was measured at a clonal age between 25 and 30 years. Heights of progenies were assessed at an age of 8 and 18 years, respectively. Exclusively descriptive statistics were employed.

Some results have been previously published with respect to graftings (Holzer 1989) and progenies (Holzer 1978). Recently, growth of vegetative and generative plant material has been measured (Feuersinger 1992).

Since altitude of timberline is irregular within the Alps, comparisons are based on relative distances to local timberline.

RESULTS AND DISCUSSION

Results are summarized in figures 1-3 within the main distribution (about 150 m below to 100 m above timberline); mean height of 30-year-old graftings decreased with increasing elevation of origin from 3.8 m at 150 m below to 2.7 m at 100 m above timberline. Variation was high and yielded to 50 to 70 percent of the clonal mean. In general, the majority of graftings originating below timberline had superior growth. Presumably, inherent growth capacity shows a cline within the main distribution zone of stone pine (fig. 1).

This growth pattern was also found in generative plant material. Progenies originating from 100 m below timberline showed pronounced reduced growth. However, when growth was only evaluated within a single seed zone, it was always higher below the timberline than above (fig. 2). In the nursery, height of families ($n = 50$) originating from production forests averaged 46.5 cm. Families ($n = 16$) from the "Kampfzone" had a slightly reduced growth of 40.0 cm at an age of 8 years.

Transplants of families 18 years old showed different results. Clinal growth pattern is still distinguishable at site 1 (400 m above sea level) and site 2 (250 m below timberline). However, at site 3 (timberline) height growth reactions were different. Here, families with small height growth potential at 400 m above sea level were superior. Figure 3 shows growth of families originating from two different seed zones. In seed zone "Defreggen" growth of 18 families, 400 m and 1,700 m above sea level, was negatively correlated ($r = -0.752^{***}$). Fourteen families originating from seed zone "Prankerhöhe" showed a consistent pattern. However, correlation ($r = -0.205$) was not significant.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Kurt Holzer is Professor of Forest Genetics, Institut für Waldbau, Universität für Bodenkultur, A-1190 Vienna, Austria.

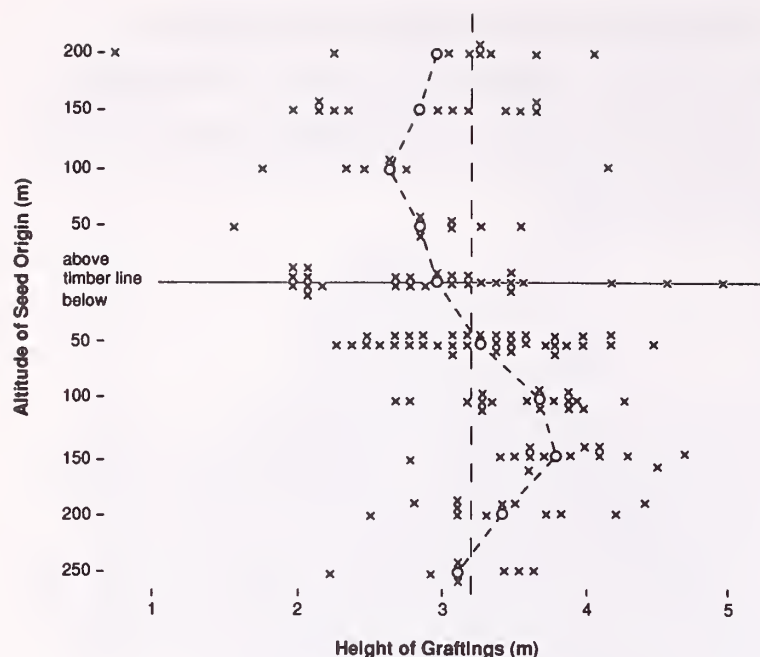


Figure 1—Total height growth of 30-year-old graftings in the plantation at 400 m above sea level with the altitude of their origin (distance from the local timberline). Dotted curve denotes the mean values.

This observation is supported by a sowing trial 200 m above local timberline (2,100 m above sea level). Progenies originating from sites above timberline performed well; progenies from trees in production forests performed poorly (Holzer 1975).

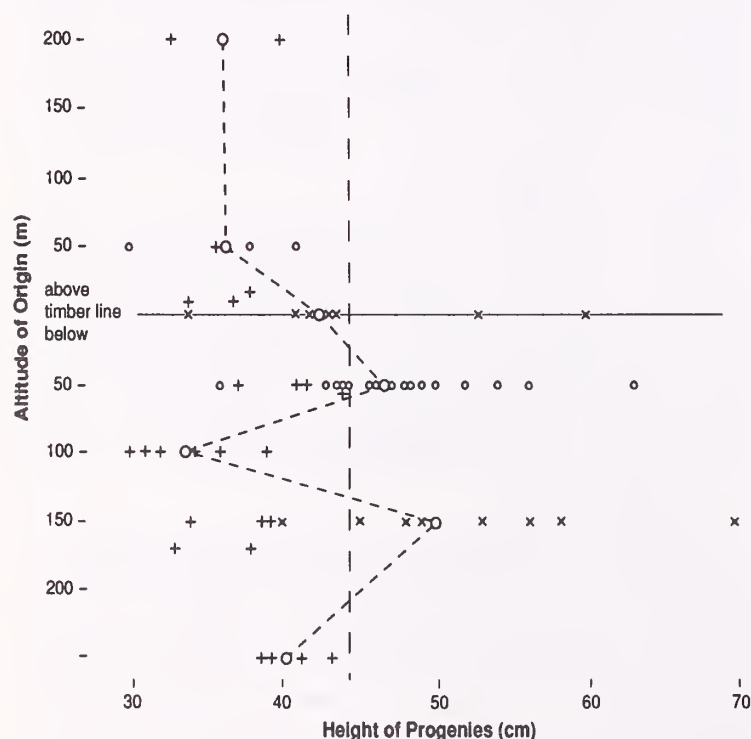


Figure 2—Total height of the 8-year-old progenies (mean of families) of the harvested clones with the altitude of their origin (distance from the local timberline). Dotted curve denotes the mean values.

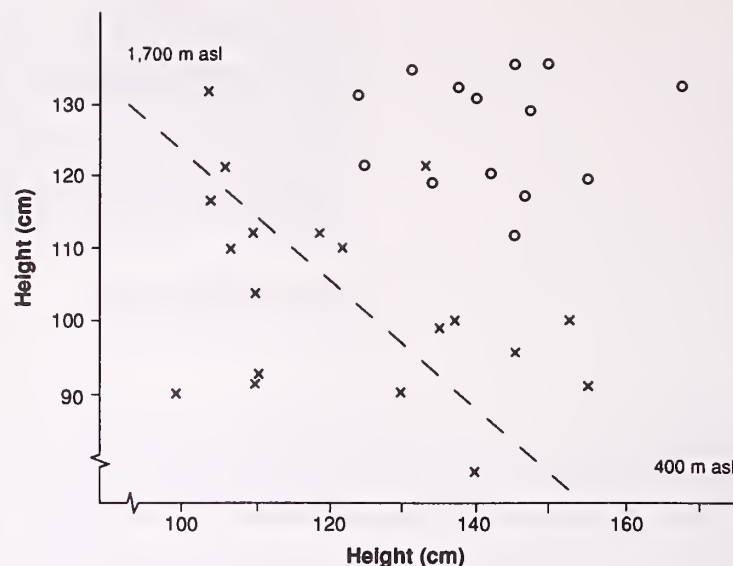


Figure 3—The comparison of the mean of the 18-year-old families on two different planting sites: 400 m and 1,700 m above sea level, respectively (provenance 1/6/100, Prankenhöhe, marked with o, provenance 1/8/100, Defreggen, marked with x; see text also). Curve denotes correlation ($r = -0.752$) of the Defreggen zone.

What conclusions regarding growth of stone pine might be drawn from these experiments so far?

1. Height growth of stone pine shows clinal variation.
2. When plants are grown in production forests, growth is positively correlated to elevation.
3. Above timberline this correlation is negative.

REFERENCES

- Feuersinger, P. 1992. Das Wachstum von Zirbe in Abhängigkeit vom Ursprungsort. Diplomarbeit, Univ. f. Bodenkultur, Wien. 140 p.
- Holzer, K. 1961. Der derzeitige Stand der Auswahl von Schwarzerlen und von Zirbe im Rahmen der Forstpflanzenzüchtung. Informationsdienst 50, Allg. Forstztg. 72.
- Holzer, K. 1963. *Pinus cembra* L. as a pioneer at timberline in the European Alps. Proc. World. Cons. Forest Genet. and Tree Imprv., Vol. 1 (FAO/FORGEN 1963, 3/13, FAO, Rome).
- Holzer, K. 1969. Erste Ergebnisse von Zirbenauswahlbäumen (*Pinus cembra* L.). Centrbl.f.d. ges. Forstwes. 86: 149-160.
- Holzer, K. 1975. Genetics of *Pinus cembra* L. Annales Forestales, Zagreb. 6(5): 139-158.
- Holzer, K. 1976. Breeding haploxyton pines for subalpine regions. XVI IUFRO-Congr. Oslo. Div. II: 216-227.
- Holzer, K. 1978. Versuchsanlage Große Zirbenwiese. Exk. Führer Arbeitsgem. f. Hochlagenaufforstung. 5 p. [Mimeo.]
- Holzer, K. 1989. Drei Jahrzehnte Erfahrungen mit Zirbenpflanzungen. Centrbl. f.d. ges. Forstwes. 106: 79-88.

SEASONAL PATTERNS OF GROWTH AND PHOTOSYNTHETIC ACTIVITY OF *PINUS PUMILA* GROWING ON THE KISO MOUNTAIN RANGE, CENTRAL JAPAN

Takuya Kajimoto

Abstract—Seasonal patterns of growth and photosynthesis in *Pinus pumila* needles were investigated in relation to carbon uptake. Current needles elongated from July to late August. Photosynthetic activities of 2-year-old needles, both in sun- and shade-needles, reached seasonal maxima in August, while those of current needles did so in September. The results suggest that annual net carbon gain of *P. pumila* depended mainly on net photosynthesis of old needles (1 to 4 year olds).

Growth and production rates of trees within the timberline ecotone are generally restricted mainly due to the short growing season (Tranquillini 1979). However, most of the subalpine species show physiological adaptations to conditions associated with low temperature, lower photosynthetic optimum temperature (Larcher 1975), and higher frost and freezing resistance (Sakai and Larcher 1987). It has also been suggested that within krummholz mats consisting of *Picea engelmannii* and *Abies lasiocarpa* photosynthesis is enhanced by more favorable canopy-temperature conditions (Hadley and Smith 1987). Information on such physiological and structural functions is indispensable for understanding how alpine trees survive by achieving positive carbon balance during the short summers.

In Japan, *Pinus pumila* Regel. occurs in high-mountain areas from central Honshu (the main island) to the northern island of Hokkaido. This pine generally exhibits dwarfed growth forms, and regenerates by layering at the mature growth stage (Kajimoto 1992; Okitsu and Ito 1984). The physiognomy of *P. pumila* is similar to *Pinus mugo* at the upper timberline in the European Alps or in the Carpathian Mountains (Holtmeier 1973, 1981; Wardle 1977).

The foliage biomass of *P. pumila* ranges from 15 to 24 tons d.w./ha despite the low tree heights. *Pinus pumila* stands develop dense canopies with leaf area density of about 5 m²/m³, which is considerably more than in other conifer forests (Kajimoto 1989a). This canopy structure may result in large annual net production (Okitsu and Ito 1989; Shidei 1963). However, seasonal changes in growth

and photosynthesis of *P. pumila* needles are still unknown in relation to their carbon uptake.

In this paper, a process of photosynthetic production in *P. pumila* during the growing season is discussed based on observations of environmental factors and seasonal patterns of growth and photosynthesis in the needles.

STUDY AREA

The study area is located on the Kiso Mountain Range in central Japan. The range trends from south to north. The highest peak is Mount Kisokoma (2,965 m a.s.l.). In this mountain range, *P. pumila* trees naturally occur above 2,500 m. The study was carried out in the Shinshu University Experimental Forest (35°48' N., 137°50' E.) in the northern part of the Kiso Mountain Range. The investigated pine stand is located on the northeast slope (15° inclination) at an altitude of 2,600 m a.s.l. Dense canopy layer is developed between 100 and 200 cm above the ground height (Kajimoto 1989a).

FIELD OBSERVATIONS

Four sun-exposed terminal shoots of *P. pumila* were selected. Lengths of current shoots, current needles, and winter buds were measured seven times between late May and October 1988. Current needle length of each shoot was determined as the average of 10 fascicles selected at equidistant intervals along the shoot axis.

At the plot, solar irradiance (400-1,100 nm in wavelength) above the canopy surface was measured with a pyranometer sensor (LICOR, LI-200SB) at 1-hour intervals from June to October 1988. Photosynthetic photon flux density (PPFD) (400-700 nm) above the canopy surface and air temperature inside the stand were also recorded at 1-hour intervals between mid-July and October 1988 using a quantum sensor (Koito, IKS-25) and a resistance thermometer (Koito, OPT-150).

MEASUREMENT OF PHOTOSYNTHESIS

Rates of CO₂ exchange were determined on detached shoots that were collected 50 hours prior to the measurement. The shoots were carefully transported to the laboratory to minimize error associated with excision and transportation (Kajimoto 1990). An open system

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Takuya Kajimoto is a special Researcher of Science and Technology, Laboratory of Plant Production, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305, Japan.

with an infrared gas analyzer (Hartmann and Braun, URA-2) was used. The air was fed into an assimilation chamber (9 by 25 by 1 cm³) at a rate of 0.5 l/min. CO₂ concentration of the input air was within the range of 360–400 ppm. The chamber was placed in a thermoregulated waterbath and illuminated with incandescent lamps. PFD at the chamber surface was measured with a quantum sensor (LICOR, LI-190SB). Details of the system were described by Kajimoto (1990).

Two terminal shoots (about 10 cm in length) of *P. pumila* were sampled from the sun-exposed canopy surface part (1.8–2.0 m) and in the lower shaded canopy layer (1.0–1.2 m) seven times between late May and October 1988. At each sampling time, about 26 fascicles of current needles (flushed in 1988) and 2-year-old needles (flushed in 1986) were separately removed from each sun- and shade-shoot. The needles were placed in the assimilation chamber keeping the cut end of each fascicle immersed in water using a small vinyl tube. Net photosynthetic rates at different PFD levels (20–1,300 $\mu\text{mol}/\text{m}^2/\text{s}$) and dark respiration rates of these two needle groups were measured. Air temperature inside the chamber was maintained at 10 °C throughout the measurement; this temperature value was within the range of optimum air temperature (10–15 °C) in net photosynthesis for *P. pumila* needles (Kajimoto 1990).

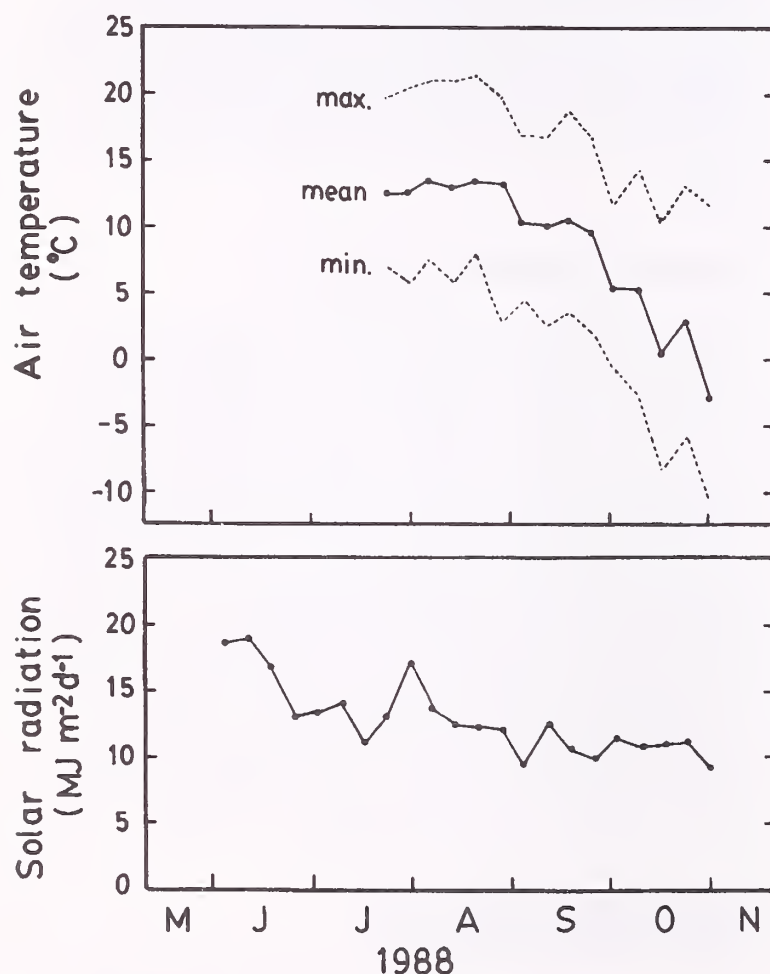


Figure 1—Seasonal changes in daily solar irradiance (400–1,100 nm in wavelength) and air temperatures during 1988 measured in a *P. pumila* stand (2,600 m a.s.l.), Kiso Mountain Range. Each point stands for the mean value at 1-week intervals.

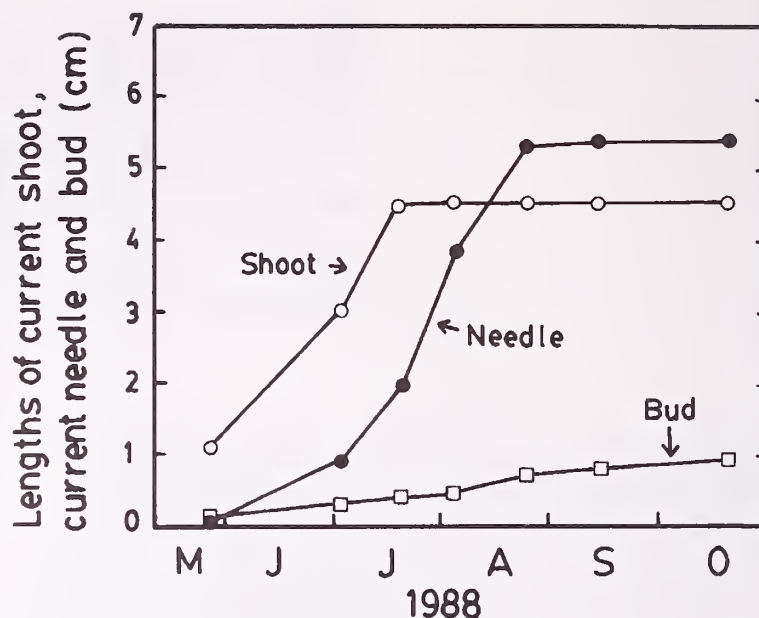


Figure 2—Seasonal growth patterns of current shoots, current needles, and winter buds observed for sun-exposed *P. pumila* shoots. Each point shows the mean for $n = 4$ shoots. \circ = shoot length; \bullet = needle length; \square = bud length.

Needle area of each sample was measured as its projected area with an area meter (Hayashi, AAC-100), and its dry weight was measured after oven-drying at 85 °C. Specific leaf area (SLA; cm²/g) was determined as the ratio of needle area to dry weight. Net assimilation rates obtained in all measurements were converted to the values at a CO₂ concentration of 380 ppm.

RESULTS

Climatic Conditions

Daily solar radiation at the *P. pumila* stand was higher in June and gradually decreased until October in 1988 (fig. 1). Mean air temperature was about 12 °C during August and fell below 0 °C after mid-October. Monthly precipitation was 212 mm in July and 167 mm in August 1988, according to the data obtained at Senjougiki Station (2,623 m a.s.l.) in the central part of Kiso Mountain Range (Nagano Meteorological Observatory 1988).

Growth Patterns of Shoots and Needles

The current shoots elongated rapidly from June to July (fig. 2). The current needles began to flush in early July and elongated rapidly during August. In late May, the winter buds, which would flush in the next season, were visible. The length of winter bud increased gradually until late October.

Specific leaf area (SLA) of the current needles, both sun- and shade-needles, was quite large in early August when the needles began to grow larger, and sharply decreased by mid-September (fig. 3). SLA of 2-year-old

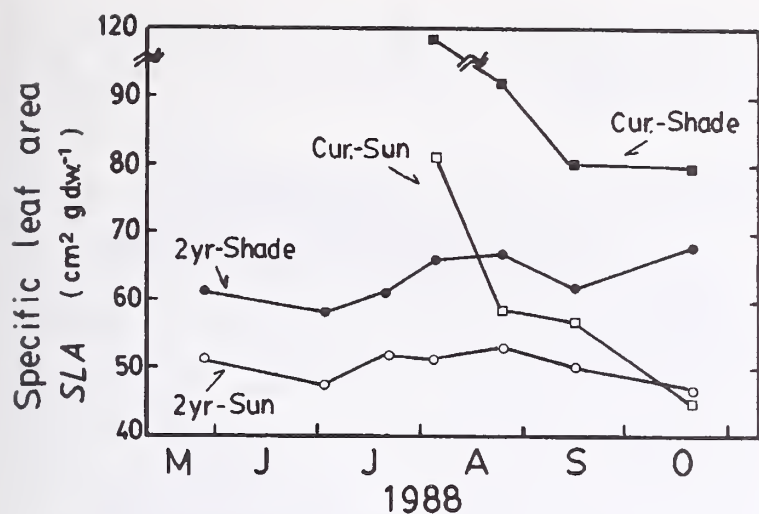


Figure 3—Seasonal changes in specific leaf area (SLA) of the *P. pumila* needles used for photosynthesis measurements. □ = current, sun-needles; ■ = current, shade-needles; ○ = 2-year-old, sun-needles; ● = 2-year-old, shade-needles.

needles became slightly larger in August than in other months. The shade-needles, both current and 2-year-old, showed larger SLA values throughout the season than sun-needles.

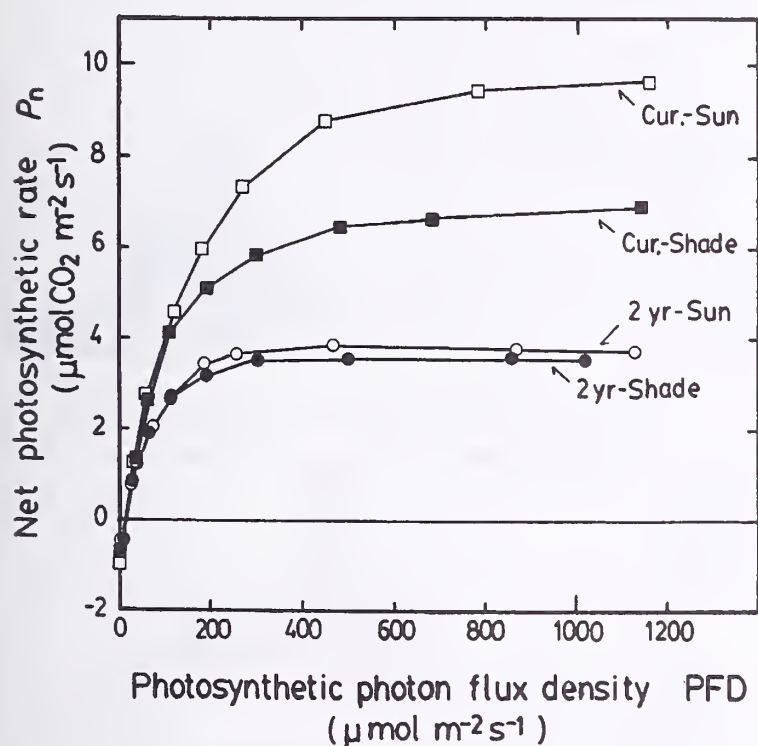


Figure 4—Examples of the relationships between photosynthetic photon flux density (PPFD) and net photosynthetic rate (P_n) at 10 °C of *P. pumila* needles on September 15, 1988. □ = current, sun-needles; ■ = current, shade-needles; ○ = 2-year-old, sun-needles; ● = 2-year-old, shade-needles.

Light Response of Net Photosynthesis

Light response of photosynthesis was examined based on the relationships between photon flux density (PPFD) and net photosynthetic rates (P_n) at 10 °C (fig. 4). Light saturation points of P_n were different between sun- and shade-needles, and also between needles of different age. However, all sampled needles were completely light saturated in P_n at PPFD value below 1,000 $\mu\text{mol}/\text{m}^2/\text{s}$ and 10 °C. A maximum net photosynthetic rate (P_{max}) was defined as P_n value at 1,000 $\mu\text{mol}/\text{m}^2/\text{s}$ and 10 °C, and an approximate light-saturation point in net photosynthesis (PPFD_{90}) was also determined as PPFD value that gave 90 percent of P_{max} .

Table 1 shows that PPFD_{90} of 2-year-old needles ranged from 180 to 500 $\mu\text{mol}/\text{m}^2/\text{s}$ in sun-needles and 180 to 440 $\mu\text{mol}/\text{m}^2/\text{s}$ in shade-needles. The values were relatively lower than those of the current needles, where PPFD_{90} was 440-580 $\mu\text{mol}/\text{m}^2/\text{s}$ in sun-needles and 300-500 $\mu\text{mol}/\text{m}^2/\text{s}$ in shade-needles. Both current and 2-year-old needles had highest PPFD_{90} values in August compared to the other months.

Seasonal Change in Photosynthetic Activity

Figure 5 shows that P_{max} of current needles were larger in sun-needles than in shade-needles for each period. For 2-year-old needles, there was a remarkable difference in P_{max} between sun- and shade-needles in July and August. The values of sun- and shade-needles both became higher in August than in other months. P_{max} values of current needles increased between late August and mid-September.

Dark respiration rates at 10 °C (R) of current needles were larger in sun-needles than in shade-needles, while there were no differences in 2-year-old sun- and shade-needles (fig. 5). Current needles showed larger R values than 2-year-old needles throughout the season.

Table 1—Approximate light-saturation points (PPFD_{90}) in the net photosynthetic rates (at 10 °C) of *P. pumila* needles in 1988

Date	Light-saturation points (PPFD_{90}) ¹ ($\mu\text{mol}/\text{m}^2/\text{s}$)			
	Current needles		2-year-old-needles	
	Sun	Shade	Sun	Shade
May 27	—	—	420	440
July 2	—	—	340	340
July 20	—	—	300	300
August 4	500	500	500	380
August 24	580	460	480	380
September 15	440	360	180	180
October 20	500	300	240	220

¹ PPFD_{90} was defined as the value of photosynthetic photon flux density which gave 90 percent of a maximum net photosynthetic rate (P_{max}). Each PPFD_{90} value was determined using the light-photosynthetic curve, as shown in figure 4.

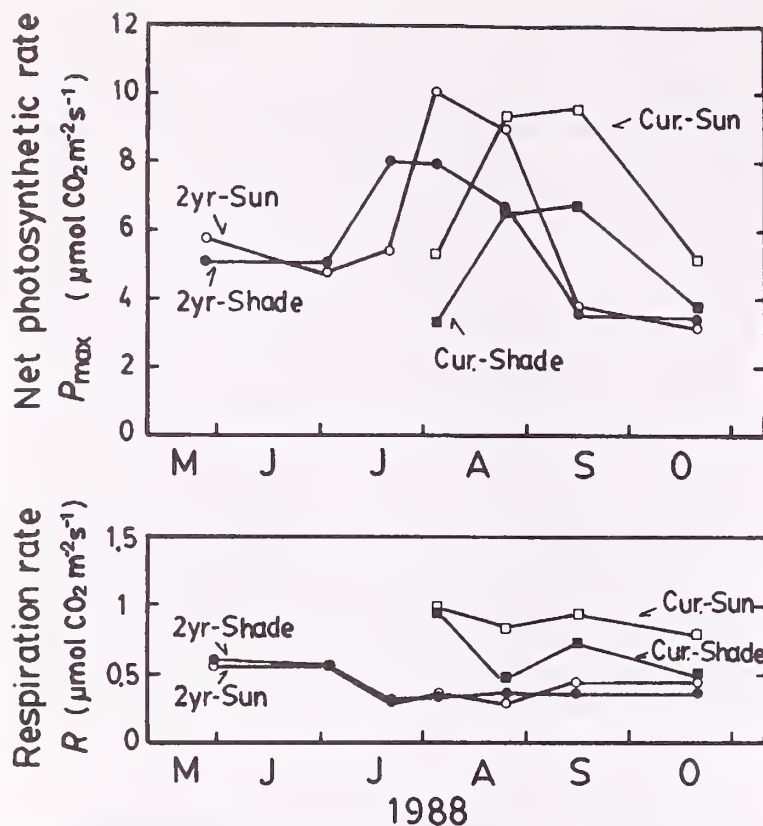


Figure 5—Seasonal changes in net photosynthetic rates (P_{\max}) at $1,000 \mu\text{mol}/\text{m}^2/\text{s}$ and 10°C , and dark respiration rates (R) at 10°C of *P. pumila* needles during 1988. \square = current, sun-needles; \blacksquare = current, shade-needles; \circ = 2-year-old, sun-needles; \bullet = 2-year-old, shade-needles.

DISCUSSION

Growth Characteristics of Needles

Needles of *P. pumila* began to elongate in early July and almost finished growth in late August (fig. 2). The period of needle growth is 1 or 2 months later than those of other low-altitude pines, for example, *P. densiflora* (Tanaka and others 1976) and *P. thunbergii* (Nagatsu 1987), growing naturally in central Japan. After needle growth had terminated, the current needles of *P. pumila* showed gradual decline in specific leaf area (SLA) (fig. 3) and maintained higher dark respiration rates than 2-year-old needles (fig. 5). This indicates that the current needles continued to accumulate internal carbohydrate or nutrient until October.

In the study area, there was little local variation in seasonal growth patterns in the shoots and needles of *P. pumila* (Kajimoto 1989b). However, the final lengths of current shoots and needles became smaller with increasing altitude, as reported for other high-altitude pines, such as *P. cembra* (Baig and Tranquillini 1976), and *P. mugo* and *P. contorta* (Benecke and Havranek 1980).

The current needles of *P. pumila* in the research plot accounted for 9 percent of total foliage biomass in late July and 27 percent in late August (Kajimoto 1989a). This indicates that 70 percent or more of the pine canopy consisted of older needles throughout the growing season.

Needle longevity of *P. pumila*, 4 years or more, corresponds to that of *P. mugo* and *P. contorta* (Benecke and Havranek 1980).

Climate Factors Affecting Photosynthetic Production

Seasonal differences in photosynthetic activity between new and old needles have been reported for some northern or subalpine evergreen conifers (Fry and Phillips 1977; Teskey and others 1984). Likewise, photosynthetic activity (P_{\max}) in the 2-year-old needles of *P. pumila* became higher between late July and early August, while that of current needles did so in late August and mid-September (fig. 5). A similar seasonal trend in P_{\max} was found for the current and older needles (1 to 4 years old) of *P. pumila* in the study plot in 1987 (Kajimoto 1990). These results suggest that photosynthetic production of the *P. pumila* canopy is primarily active during August and September.

Alpine conifer trees rarely achieve their potential maximum photosynthetic activities under natural environmental conditions, although the main limiting factors in photosynthesis, such as irradiance and air and soil temperatures, seem to be different depending on species and site conditions (De Lucia and Smith 1987; Häslér 1982; Turner and others 1983). Mean air temperatures between late July and mid-September at the research plot (fig. 1) corresponded to optimum air temperature ($10\text{--}15^\circ\text{C}$) for net photosynthesis of *P. pumila*, both for current and old

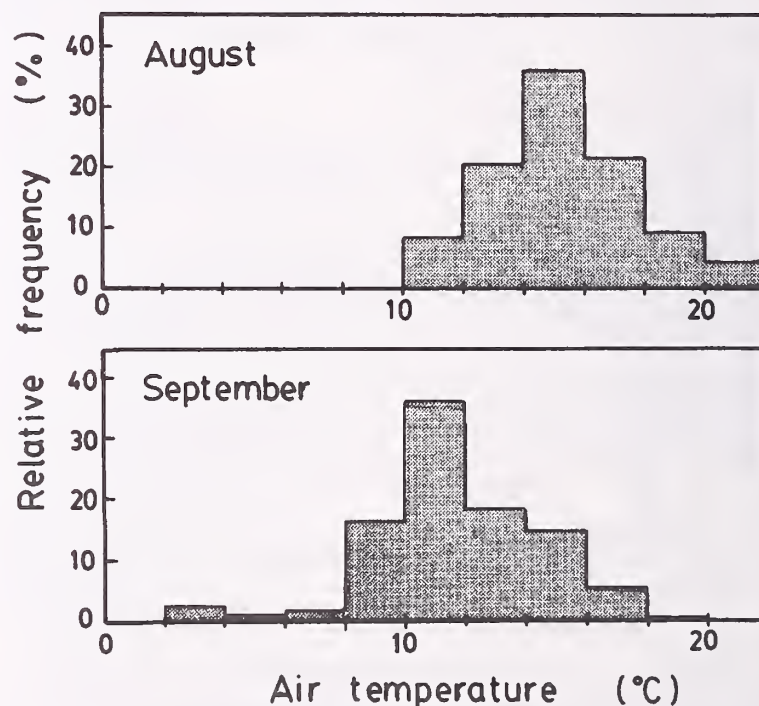


Figure 6—Relative frequency distributions of daytime (8 a.m. to 4 p.m.) mean air temperature at each 1-hour interval in August (above) and September (below) 1988. Air temperatures were recorded at the *P. pumila* stand (2,600 m a.s.l.), Kiso Mountain Range.

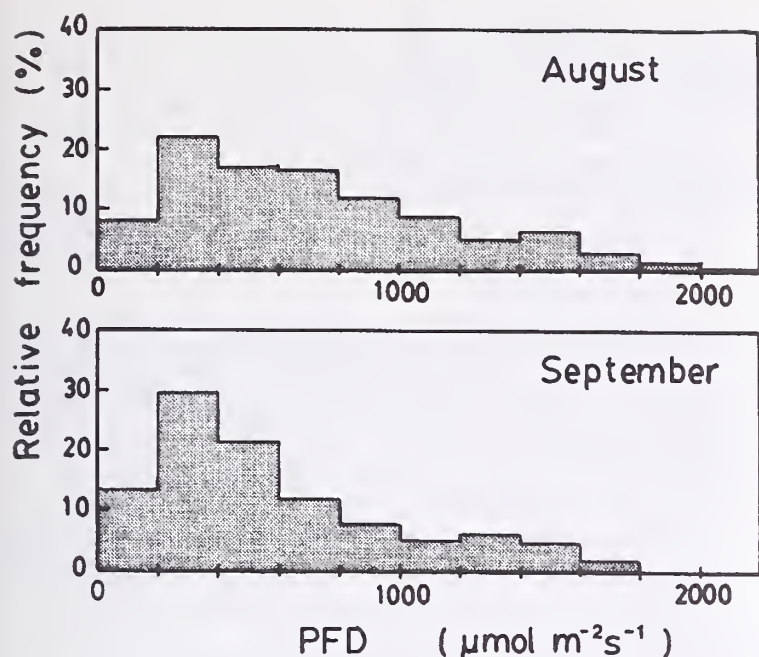


Figure 7—Relative frequency distributions of daytime (8 a.m. to 4 p.m.) photosynthetic photon flux density (PPFD) at each 1-hour interval in August (above) and September (below) 1988. PPFD was measured above the canopy surface of *P. pumila* stand (2,600 m a.s.l.), Kiso Mountain Range.

needles (Kajimoto 1990). Figure 6 shows patterns of relative frequency distribution of daytime mean air temperature (8 a.m. to 4 p.m.) at 1-hour intervals; temperature values between 10 and 16 °C made up about 70 percent of the sum total in both August and September. With regard to irradiance conditions, proportions of PPFD values above 600 $\mu\text{mol}/\text{m}^2/\text{s}$, when the pine needles were photosynthetically light saturated (table 1), were 53 percent in August and 36 percent in September (fig. 7). The temperature and light regimes indicate that net assimilation of *P. pumila* needles under natural conditions is limited mainly by lower levels of solar irradiance. Reduction in available PPFD from August (53 percent) to September (36 percent) is likely to impede net photosynthesis of the current needles, since photosynthetic activities (P_{max}) of the current needles were the highest in September (fig. 5).

It is concluded from the present study that *P. pumila* needles are not very efficient in photosynthesis during the first growing season. The pine needles survive for four or more growing seasons and recover their photosynthetic abilities in each summer; P_{max} of the oldest needles (4 years old) was about half of that of 1-year-old needles, although P_{max} decreased with needle age (Kajimoto 1990). Consequently, a large proportion of annual net carbon gain in the *P. pumila* tree is likely to depend on net assimilation by the old needles.

Knowledge of physiological properties of *P. pumila*, especially water relations (Ando and Kawasaki 1991), is still limited compared to other subalpine pine species. As to seasonal photosynthetic production of *P. pumila*, more information on its photosynthetic responses to environmental factors, particularly based on field measurement, is needed.

ACKNOWLEDGMENTS

I thank Dr. K. Hozumi for his suggestions and encouragement during this study, and Drs. T. Koike, M. Ishizuka, A. Osawa, Y. Chiba, and N. Kurachi for their useful comments on this manuscript. Comments by Drs. F.-K. Holtmeier, W. C. Schmidt, and R. Häsler are acknowledged. Thanks also go to Professors T. Horiuchi and S. Ito, Shinshu University, and to the staff of Shinshu University Experimental Forest and of Nagoya University Forest for their assistance during the field survey.

REFERENCES

- Ando, H.; Kawasaki, K. 1991. Growth of *Pinus pumila* in relation to the site conditions on a slope. Transactions of the 102d Meeting, Japanese Forestry Society: 451-452. [In Japanese].
- Baig, M. N.; Tranquillini, W. 1976. Studies on upper timberline: morphology and anatomy of Norway spruce (*Picea abies*) and stone pine (*Pinus cembra*) needles from various habitat conditions. Canadian Journal of Botany. 54: 1622-1632.
- Benecke, V.; Havranek, W. M. 1980. Phenological growth characteristics of trees with increasing altitude, Craigieburn Range, New Zealand. In: Benecke, U.; Davis, M. R., eds. Mountain environments and subalpine tree growth. Tech. Pap. 70. New Zealand Forest Service, Forest Research Institute: 155-174.
- De Lucia, E. H.; Smith, W. K. 1987. Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. Canadian Journal of Forest Research. 17: 527-533.
- Fry, D. J.; Phillips, I. D. J. 1977. Photosynthesis of conifers in relation to annual growth cycles and dry matter production. II. Seasonal photosynthetic capacity and mesophyll ultrastructure in *Abies grandis*, *Picea sitchensis*, *Tsuga heterophylla* and *Larix leptolepis* in S.W. England. Physiologia Plantarum. 40: 300-306.
- Hadley, J. L.; Smith, W. K. 1987. Influence of krummholz mat microclimate on needle physiology and survival. Oecologia. 73: 82-90.
- Häsler, R. 1982. Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. Oecologia. 54: 14-22.
- Holtmeier, F.-K. 1973. Geoecological aspects of timberlines in northern and central Europe. Arctic and Alpine Research. 5(3): 45-54.
- Holtmeier, F.-K. 1981. What does the term "krummholz" really mean? Observations with special reference to the Alps and the Colorado Front Range. Mountain Research and Development. 1(3/4): 253-260.
- Kajimoto, T. 1989a. Aboveground biomass and litterfall of *Pinus pumila* scrubs growing on the Kiso Mountain Range in central Japan. Ecological Research. 4: 55-69.
- Kajimoto, T. 1989b. Current growth of *Pinus pumila*. Transactions of the 37th Meeting, Chubu Branch, Japanese Forestry Society: 55-58. [In Japanese].
- Kajimoto, T. 1990. Photosynthesis and respiration of *Pinus pumila* needles in relation to needle age and season. Ecological Research. 5: 333-340.

- Kajimoto, T. 1992. Dynamics and dry matter production of belowground woody organs of *Pinus pumila* trees growing on the Kiso Mountain Range in central Japan. *Ecological Research*. 7: 333-339.
- Larcher, W. 1975. *Physiological plant ecology*. Heidelberg: Springer. 252 p.
- Nagano Meteorological Observatory. 1988. Annual report on weather conditions of Nagano prefecture in 1987. Nagano Branch Office of Japanese Meteorological Society. 137 p. [In Japanese].
- Nagatsu, M. 1987. Correlation between the growth of needles and shoots in a *Pinus thunbergii* young tree. *Transactions of the 98th Meeting Japanese Forestry Society*: 417-418. [In Japanese].
- Okitsu, S.; Ito, K. 1984. Vegetation dynamics of the Siberian dwarf pine (*Pinus pumila* Regel) in the Taisetsu Mountain Range, Hokkaido, Japan. *Vegetatio*. 58: 105-113.
- Okitsu, S.; Ito, K. 1989. Conditions for the development of the *Pinus pumila* zone of Hokkaido, northern Japan. *Vegetatio*. 84: 127-132.
- Sakai, A.; Larcher, W. 1987. Frost survival of plants. *Ecol. Stud.* 62. New York: Springer. 321 p.
- Shidei, T. 1963. Productivity of Haimatsu (*Pinus pumila*) community growing in alpine zone of Tateyam-Range. *Journal of the Japanese Forestry Society*. 45: 169-173. [In Japanese with English summary].
- Tanaka, H.; Oohata, S.; Akai, T. 1976. Elongation and shoot forms in foreign pines. Report, Kyoto University of Forestry. 11: 38-49. [In Japanese].
- Teskey, R. O.; Grier, C. C.; Hinckley, T. M. 1984. Changes in photosynthesis and water relations with age and season in *Abies amabilis*. *Canadian Journal of Forest Research*. 14: 77-84.
- Tranquillini, W. 1979. *Physiological ecology of the alpine timberline*. *Ecol. Stud.* 31. New York: Springer. 131 p.
- Turner, H.; Häsler, R.; Schönenberger, W. 1983. Contrasting microenvironments and their effects on carbon uptake and allocation by young conifers near alpine treeline in Switzerland. In: Wareing, R. H., ed. *Carbon uptake and allocation in subalpine ecosystems as a key to management: Proceedings of IUFRO workshop*. 1982 August 2-3. Corvallis, OR: Oregon State University, Forest Research Laboratory: 22-30.
- Wardle, P. 1977. Japanese timberlines and some geographic comparisons. *Arctic and Alpine Research*. 9: 249-258.

HEIGHT GROWTH IN CEMBRAN PINE AS A FACTOR OF AIR TEMPERATURE

Herbert Kronfuss

Abstract—The study treats height growth in cembran pine (*Pinus cembra*) in high-elevation afforestation at an altitude of 1,800 m with growth patterns analyzed as a factor of air temperature. It is assumed that growth behavior follows an endogenous rhythm possibly deriving from the genotype. The relationship between growth pattern and air temperature is demonstrated for defined periods and phases of height growth. From the results it becomes obvious that height growth and thus the relative rate of growth are primarily dependent on temperature. Data from long-term monitoring series were used to determine the amplitudes between the growth curves for early and for late culmination. A comparison of the amplitudes for cembran pine with spruce and larch shows cembran pine—with the highest amplitudes—to be the most sensitive to temperature. Cembran pine thus makes most efficient use of warm weather periods for increment production in short periods of time.

The cembran pine (*Pinus cembra*) occupies the highest stands of all trees in the Alps and as such is ideally suited for a study of height growth related to air temperature. The fact that cembran pine is not thought to have different ecotypes adapted to various altitudes also permits growth characteristics of this species to be defined in specific terms.

STUDY SITE

The study site was located 30 km southwest of Innsbruck, Tyrol (Austria), in the Stubai Alps near Haggen in the Sellrain Valley. For location, geology, and climate details, see figures 1 and 2, and table 1. The results relate to a continuous experimental stand of cembran pine at an altitude of 1,800 m. The stand was established in 1970 when the plot was afforested with 4-year-old plants.

MONITORING

Monitoring was performed over a period of 8 years for a group of 40 trees. Height growth in cembran pine was measured at 5-day intervals (pentades) and the rate of growth correlated with mean air temperature of the pentade. Individual height increments were expressed as a percentage of annual cumulative growth to permit the growth patterns to be compared with changes in temperature.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Herbert Kronfuss is Forester, Forestry Research Institute of Austria, Rennweg 1/29, A-6020 Innsbruck.

Growth patterns are represented in the form of relative growth-rate curves and relative cumulative-growth curves. This not only permits direct comparisons to be made between annual increments but also, given a long enough monitoring period, permits a characteristic increment pattern (type) to be derived for each species (Burger 1926; Larcher 1980; Weck 1955).

HEIGHT GROWTH

From 1978 to 1985 increment growth lasted an average of 108 days, with a 20-day variance range.

To study the influence of temperature on the growth pattern during the period of extension growth, the relative growth-rate curve was correlated with the temperature curve, with the mean height increments from consecutive pentades expressed as a percentage of total height growth. The relative growth-rate curve clearly illustrates the pattern of height growth (fig. 3).

Figure 3 shows how temperature fluctuations during the period of extension growth influence the rate of height growth. With regard to the correlation between the height-growth behavior and temperature patterns, the following points would seem to be of interest.

During growing season, the temperature curve itself is characterized by two pronounced dips for the periods May 20 to 25 and June 15 to 20, a phenomenon well known to the local rural communities as the "Ice Saints" and "Sheep's Chill." At the beginning of April, mean temperature reaches freezing point on the long-term average. The rise in temperature continues until mid-May, reaching an average of approximately 7 °C, before dropping back to 5 °C for the pentade occupying the first of the two

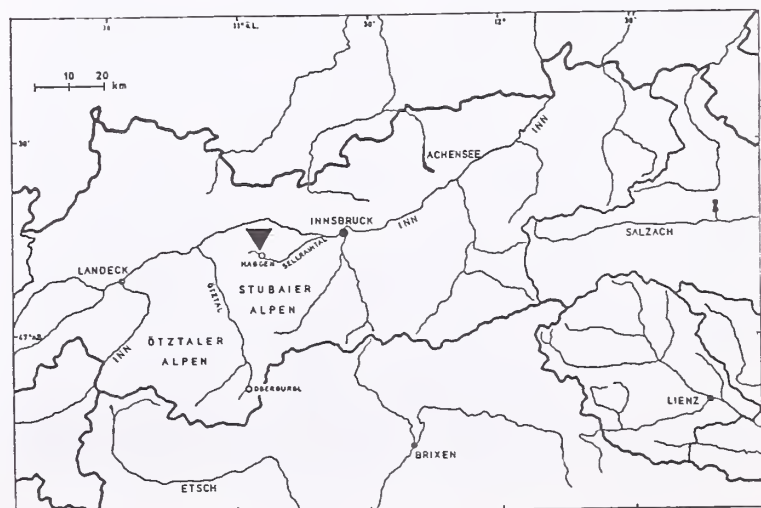


Figure 1—Geographical location of the site.

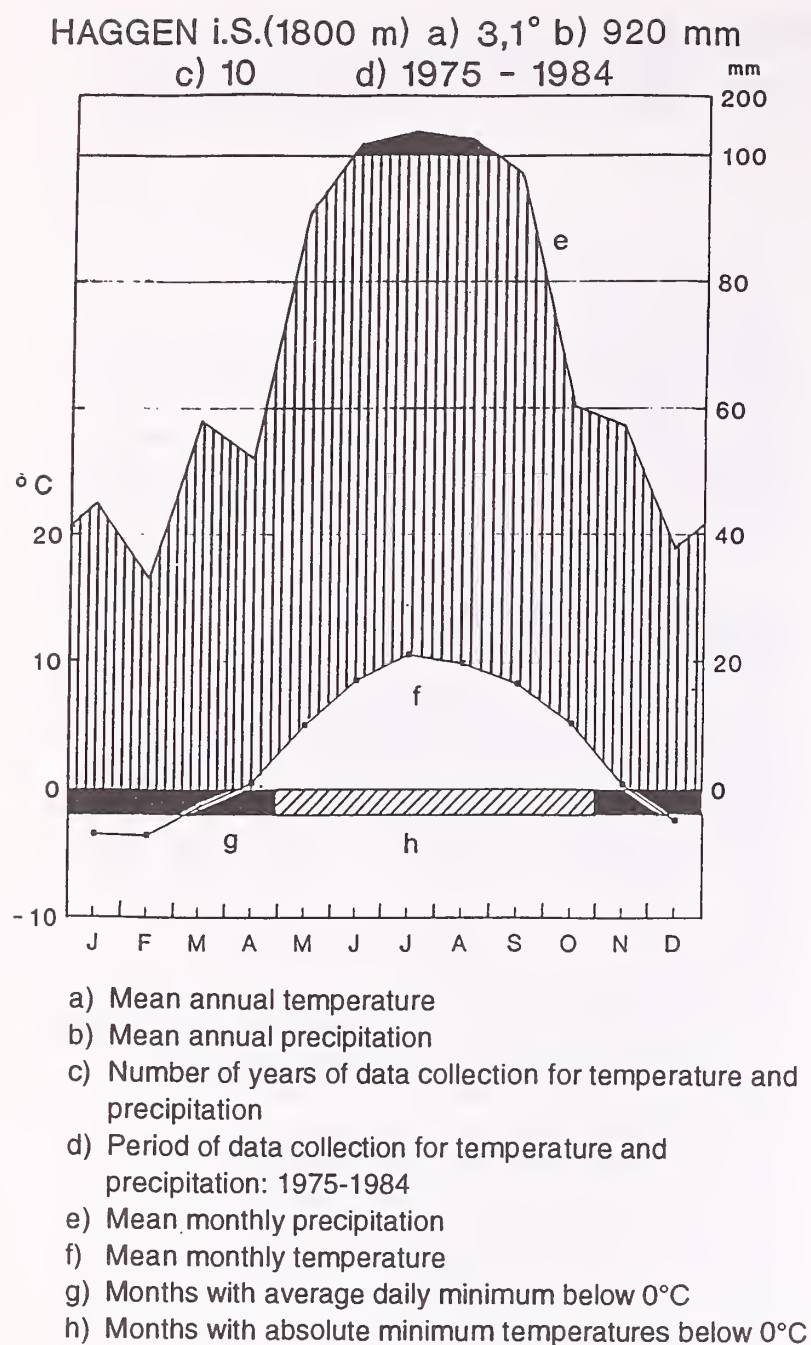


Figure 2—Data for Haggen Climate Diagram
Haggen i.S., Field Station I, 1,800 m, SSW.

cold spells. During the time of the "Ice Saints," most of the cembran pines are at the beginning of the period of extension growth, with a growth rate of only 2 to 3 percent of relative growth per pentade. That corresponds to about 1.5 cm. On the average, approximately 7 percent of cumulative growth is achieved by this point in time. For height growth in cembran pines in this location, the period between the "Ice Saints" and "Sheep's Chill" is of special importance as it includes the first major peak in the temperature curve, on or around May 31 on average.

With a brief delay, this temperature peak stimulates a response in the cembran pine in terms of height growth, and after one- and one-half pentades, the biggest absolute increment is produced, accounting for about 35 percent of

total growth on a long-term average. Following this peak in increment production, the typical pattern of height growth in the cembran pine is one of declining rates of growth in spite of rising temperatures. This is shown in figure 3 with the two curves moving in opposite directions following the start of the "Sheep's Chill" period around June 20.

Not even an increase in mean pentade temperature beyond the 10 °C mark around July 5, finally peaking at 13 °C, leads to a further spontaneous spate of growth.

Table 1—Location of the study: HAGGEN afforestation site in the Sellrain Valley near St. Sigmund, Tyrol

Geographical coordinates:	47°13'N. 11°06'E.
Height above sea-level:	1,715-1,950 m
Exposition and angle of slope:	SSW, 30°
Bedrock:	Foliated gneiss (biotite granite gneiss, granodiorite gneiss) and mica schist.
Vegetation at afforestation:	Heath (callunetum, nardetum alpinum)
Soils:	Humus horizons developed into a brown earth type through grazing and haymaking. More or less podsollic brown soils.
In previous centuries a heavily grazed avalanche slope.	
CLIMATIC DATA are based on a 10-year monitoring period (1975-1984)	
- Sunshine hours during the vegetation period (mid-May to September)	
a) theoretical asatropical maximum	2,005 hours
b) theoretical local maximum	1,393 hours
horizon loss	30.5 percent
- Air temperature	
a) mean annual temperature	3.1 °C
b) during vegetation period	8.4 °C
- Precipitation	
a) mean annual precipitation (3 m aboveground)	920 mm
b) during vegetation period (3 m aboveground)	533 mm
c) precipitation at ground level	650 mm
(= approx. 22 percent higher than at 3 m aboveground)	
- Precipitation probability (percent)	
a) June maximum	55 percent
b) December minimum	27 percent
- Mean precipitation distribution (mm)	
a) maximum in July and September	8.4 mm
b) minimum in February	3.6 mm
c) month with highest precipitation (July)	141 mm
d) month with lowest precipitation (February)	33 mm
- Evaporation during the vegetation period	
a) potential evaporation (2.5 m aboveground with "piche") (= 4.1 l/m ² per day)	566 mm
b) actual evapotranspiration (lysimeter with ground vegetation (= 1.7 l/m ² per day)	236 mm
c) actual hydrological budget	412 mm
(= 3 l/m ² per day)	

The meteorological summer semester accounts for 65 percent of annual precipitation (598 mm), and the meteorological winter semester 35 percent (322 mm).

Mean pentad values for relative growth rate
and air temperature (°C)

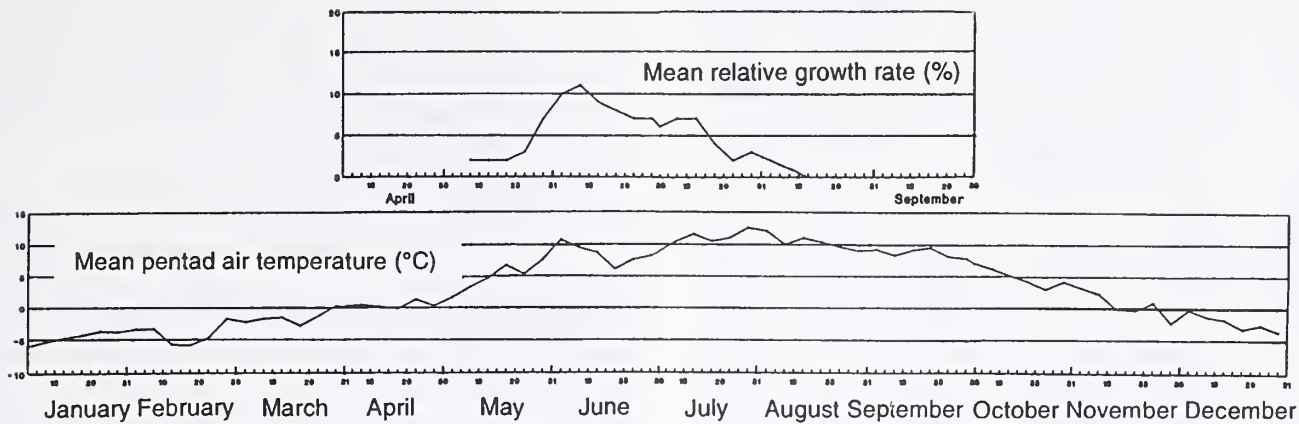


Figure 3—Comparison between the curves of relative growth rate and air temperature, 8-year series (1978 to 1985).

The minor fluctuations in the growth curve on the order of 1 to 3 percent can be correlated with temperature fluctuations of 10 to 13 °C.

The main features of the curves in figure 3 can be described as follows: The growth curve for cembran pine peaks (maximum growth rate per pentade is reached) on June 5 to 10 on average. The temperature curves are characterized by two peaks, the first between the two pronounced dips (May 31 to June 5) and the second between July 25 and July 31. It is interesting to note that height increments between July 5 and the end of the period of extension growth—and that is a good 46 days—total only 20 percent of cumulative growth, even though the temperature curve passes 10 °C on July 5 and remains more or less at that level until mid-September.

The above picture, based on the mean figures calculated from monitored data, illustrates in bold strokes the correlation between the temperature and height-growth patterns.

The relative growth-rate curves shown in figure 4 for the 8 years from 1978 to 1985 provide an overview of growth patterns in cembran pine as a factor of air temperature for the individual years. One of the more striking features of these curves is the variation in the onset of culmination (equals greatest increment production per pentade). On this basis we can distinguish between annual growth curves with early culmination (1979, 1981, 1982, 1983), one year with late culmination (1984), and years with twin or intermediate peaks (1978, 1980, 1985; see also table 2).

A comparison of the temperature curve in figure 3 with the growth-rate curves in figure 4 reveals two clearly delineated time periods in which culmination (peak growth rate per pentade) occurs. The first is the period between the “Ice Saints” and “Sheep’s Chill,” and the second is a subsequent period of 30 days ending approximately with the pentade of July 15 to 20. These two periods together total 57 days (equals 53 percent of the mean

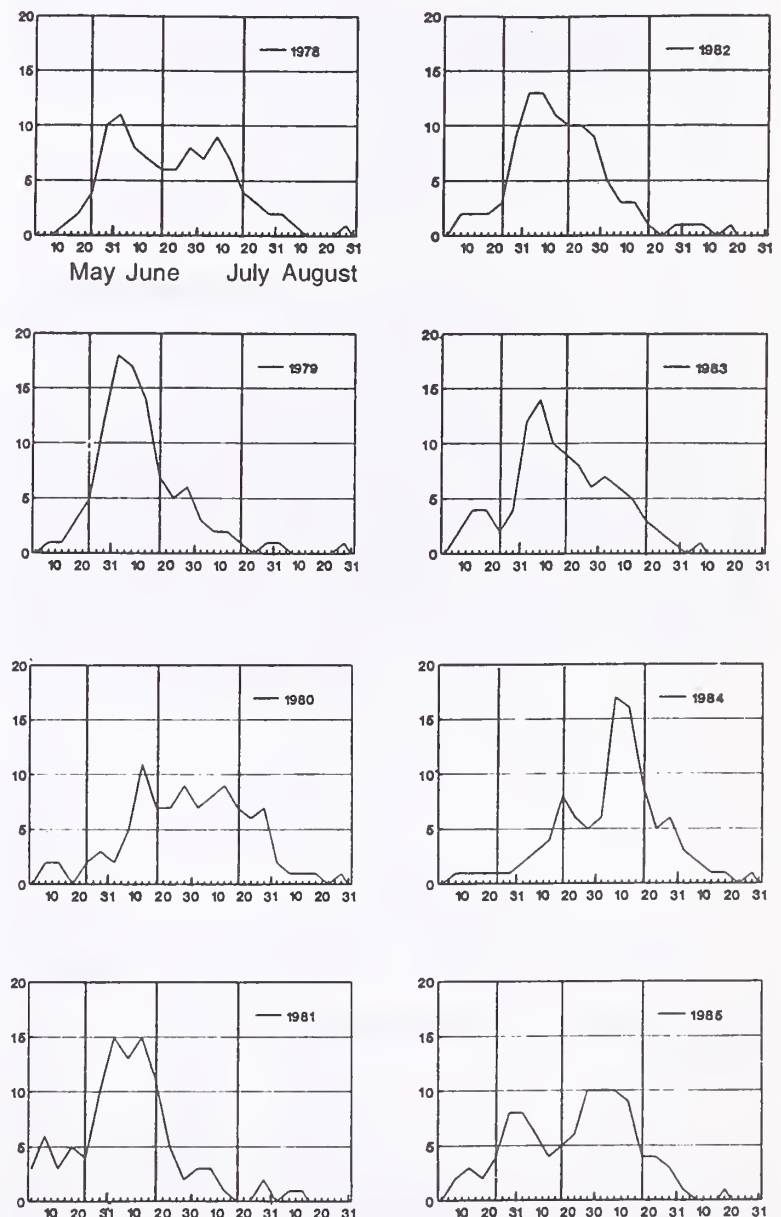


Figure 4—Cembran pine relative height-growth curves (percent).

Table 2—Air temperature in °C and percentage growth in cembran pine¹

Year	I		II		I	I
	TS	T	TS	T	HG	HG
-----°C-----						
-----Percent-----						
Early culmination						
1979	245	9.1	298	9.9	71	22
1981	242	8.9	230	7.7	61	19
1982	246	9.1	368	12.3	52	35
1983	203	7.5	359	12.0	46	38
Average	234	8.7	314	10.5	58	28
Intermediate culmination						
1978	222	8.2	241	8.0	38	52
1980	195	7.2	205	6.8	26	47
1985	191	7.1	284	9.5	31	50
Average	203	7.5	243	8.1	32	50
Late culmination						
1984	169	6.3	284	9.5	17	58

¹I = period from the "Ice Saints" to "Sheep's Chill"; II = period from "Sheep's Chill" to 20 July; TS = temperature sum; T = mean temperature; HG = height growth; period I lasts for 27 days; period II lasts for 30 days.

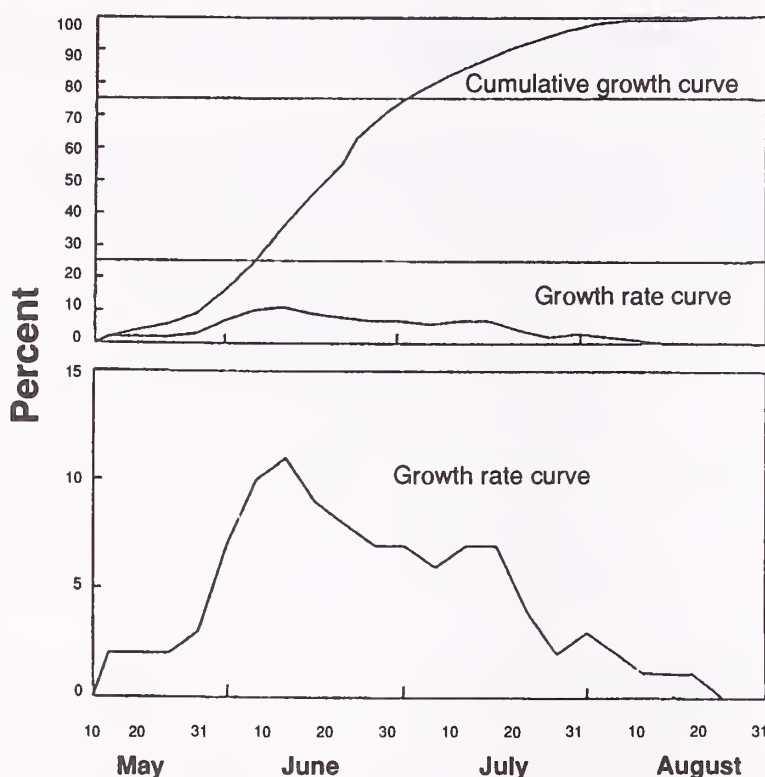


Figure 5—Cembran pine relative height growth (percent).

period of extension growth) and account for an average of 82 percent of annual shoot length.

There is a significant correlation between percentage growth within the two main growth periods and temperature sum, with peak growth located in the period that exhibits the highest temperature sum in absolute terms,

except that beyond an average temperature sum of 230 °C for the first period a further increase in temperature for the second period does not trigger higher growth rates in that period. The highest pentade growth rate always occurs in the period with the highest temperature sum and coincides with or follows the pentade with maximum pentade temperature (see table 2).

From table 2 it can be seen that in the case of early culmination the average temperature sum in the first period was 234 °C (8.7 °C/27 days). During that period, an average of 58 percent of extension growth was measured (with scatter between 46 percent and 71 percent). In those cases the cembran pines achieved an average of only 28 percent relative growth in the second period in spite of the rise in the average temperature sum to 314 °C (10.5 °C/30 days).

The year of late culmination, 1984, is also instructive. The cold weather in period I of that year produced a temperature sum of only 169 °C (6.3 °C/27 days), which is reflected in a correspondingly low relative growth rate of 17 percent. Period II, however, was characterized by a significant rise in temperature, producing a temperature sum of 284 °C (9.5 °C/30 days). The relative growth rate in that period (fig. 5) was 58 percent, which is identical with the figure for period I in the years of early culmination.

At the end of July in the late culmination year, the leaders had reached 90 percent of total extension growth compared with 98 percent for the years of early culmination.

This analysis of the height-growth patterns of cembran pine over an 8-year period of observation (1978 to 1985) shows that the cembran pine is ontogenetically equipped to make efficient use of available warmth for increment production so as to achieve culmination as early as possible. Up to that point, air temperature is the dominant factor in determining the relative growth rate, and afterward it continues to function as the "engine" that maintains the extension process.

PHASES OF HEIGHT GROWTH

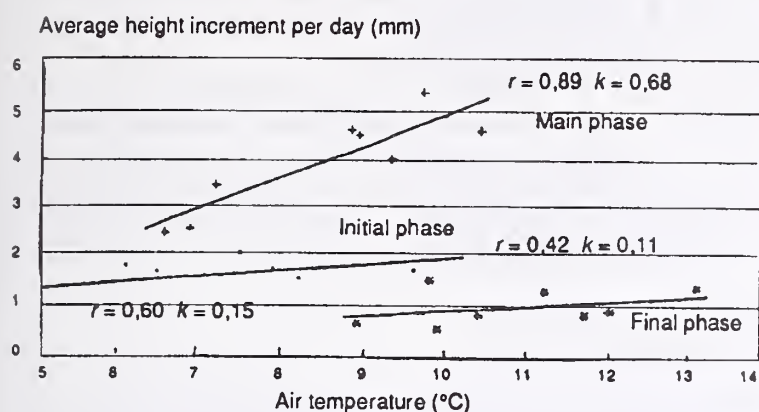
The following analysis of annual height growth by help of the growth curve (Kronfuss 1985) will illustrate the somewhat abstract correlation between growth rate and temperature with the aid of further figures. For this purpose, height growth can be divided into the following three phases (fig. 6):

- Initial phase (0 to 25 percent of annual extension).
- Main phase (25 to 75 percent of annual extension).
- Final phase (75 to 100 percent of annual extension).

Table 3 provides a separate assessment of the correlation for each of these three phases using a regression line, correlation coefficient, and regression coefficient to express the relationship between mean daily temperature (T/d) and average height growth per day (HG/d) (fig. 6, table 3).

Whereas the correlation coefficient for the initial phase ($r = 0.6$) suggests a correlation with temperature, this is no longer the case in the final phase ($r = 0.42$). The main

Correlation between mean daily air temperature and height increment per day HAGGEN i.S., 1800 m



Correlation between mean daily air temperature and growth processes HAGGEN i.S., 1800 m

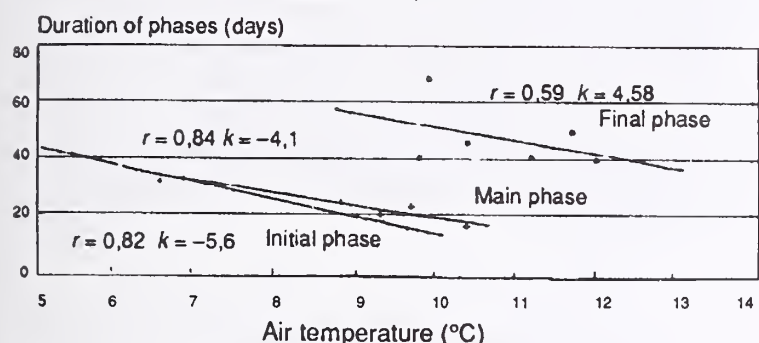


Figure 6—Cembran pine correlations between mean daily air temperatures, height increment, and duration of growth phases: period 1978 to 1985.

growth phase, on the other hand, is largely determined by temperature, as can be seen from the almost stretched curve (fig. 6 at top) and a correlation coefficient of $r = 0.89$.

The regression coefficients (k), as the expression of average daily growth per unit of temperature, show that, for the same temperature rise, height growth in the main

phase is 4.5 times greater than in the initial phase and 6.2 times greater than in the final phase. In the initial phase, with an average period of extension growth of 32 days, the average daily increment is 1.6 mm. In the main growth phase the period of extension growth is reduced to an average of 26 days of an HG/d of 4 mm, while the figure for the subsequent 50 days of the final phase is only 1 mm.

The duration of extension growth also correlates with temperature and is shorter with higher temperature rise. The influence of temperature on the period of extension growth can be seen from the correlation coefficients, with a close correlation with temperature expressed by the coefficients $r = 0.82$ for the initial phase and $r = 0.84$ for the main growth period, decreasing in the final phase to $r = 0.59$. This low correlation coefficient shows that reduced height growth in the final phase is no longer due exclusively to the influence of temperature, but to the tailing away of an endogenous pattern. With regard to the temperature-dominated phases of extension growth, (the initial and main phases) an increase in mean temperature by 1 °C reduces the extension growth period by 4 to 5 days. Also, in the final phase we see again that the pattern derives from an autonomous endogenous rhythm that determines the potential period of extension growth in this phase for the species involved.

GROWTH CURVE VARIANTS

As can be seen from the shapes of the relative growth-rate curves in figure 4, annual patterns of height growth vary considerably for the same species in the same locations. Eight years of observation offer enough data for graphic representation of maximum amplitudes between the growth curves for the earliest and those for the latest culminations and for a comparison with spruce and larch (fig. 7). This illustrates not only the time sequences with regard to flushing but also the current range of fluctuation for these tree species.

Table 3—Correlations between mean daily temperature (t°/d) and height growth per day (HG/d) and between mean daily temperature (t°/d) and the period of extension growth days (d)

Year	Initial phase ¹			Main phase ²			Final phase ³		
	t°/d	HG/d	d	t°/d	HG/d	d	t°/d	HG/d	d
1978	7.9	1.8	24	6.9	2.6	33	10.4	0.9	48
1979	9.6	1.8	22	8.8	4.7	17	9.9	.6	71
1989	5.4	.9	43	6.6	2.5	32	12.0	1.0	42
1981	6.5	1.7	25	.4	4.7	18	8.9	.7	59
1982	8.2	1.6	28	9.3	4.1	22	11.7	.9	52
1983	6.1	1.8	33	8.8	4.6	26	13.1	1.5	40
1984	5.2	1.3	52	9.7	5.5	25	9.8	1.6	42
1985	7.5	2.1	29	7.2	3.5	35	11.2	1.4	43
Average	7.1	1.6	32	8.5	4.0	26	10.9	1.1	50

¹Initial phase: correlation coefficient $r = 0.604$; regression coefficient $k = 0.147$; point of intersection $b = 0.587$; standard deviation $s = 0.326$.

²Main phase: $r = 0.889$; $k = 0.681$; $b = -1.471$; $s = 1.000$.

³Final phase: $r = 0.426$; $k = 0.117$; $b = -0.195$; $s = 0.353$.

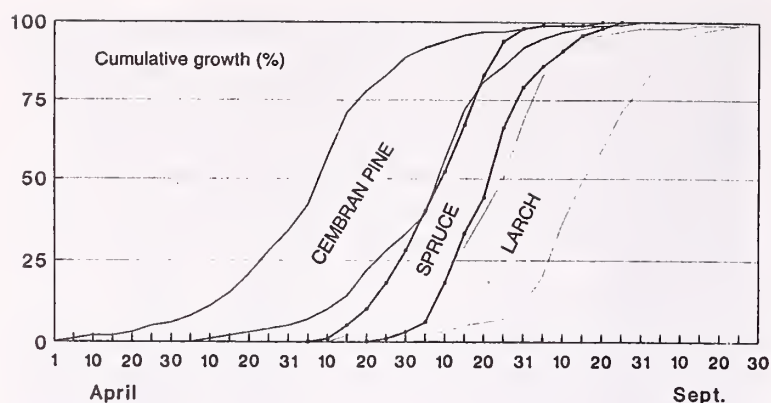


Figure 7—Characteristic growth curve amplitudes for cembran pine, spruce, and European larch: afforestation "Haggen" in 1,800 m a.s.l.

Apart from the differences in the beginning and end of the period of extension growth, cembran pine is the most sensitive to temperature of the three species, as the high amplitude shows. It can be concluded that the cembran pine makes the most efficient use of warm weather conditions for increment production. In the initial phase of

extension growth, cembran pine is already well ahead of the other species in terms of growth. In the main growth phase, larch is also surpassed by the cembran pine, while spruce comes very close to it.

For the main growth period, the two extremes of the growth curves for spruce and larch are almost parallel. This shows that increment production per pentade is more balanced between warm and cold conditions than in the case of cembran pine, which is much more sensitive to temperature fluctuations.

REFERENCES

- Burger, H. 1926. Untersuchungen über das Höhenwachstum verschiedener Holzarten. Mitt. Schweiz. Centralanst. Forstl. Vers. wesen; XIV/I.
- Kronfuss, H. 1985. Die Zuwachsleistung einer Hochlagenaufforstung mit Zirbe (*Pinus cembra*) auf einem Südhang, in Abhängigkeit von der Seehöhe. IUFRO Meeting Proceedings. Davos, Switzerland.
- Larcher, W. 1980. Ökologie der Pflanzen auf physiologischer Grundlage. Ulmer, Stuttgart.
- Weck, J. 1955. Forstliche Zuwachs und Ertragskunde. Neumann, Berlin.

SURVIVAL AND GROWTH OF PLANTED CEMBRAN PINES AT THE ALPINE TIMBERLINE

Josef Senn
Walter Schönenberger
Ueli Wasem

Abstract—In an experimental afforestation with cembran pines (*Pinus cembra* L.) at the subalpine timberline, tree survival was mainly determined by the date of disappearance of the snow cover in spring. Trees survived well on early snow-free sites and poorly on sites with long-lasting snow cover. The major causes of mortality were the two parasitic fungi *Ascocalyx abietina* and *Phacidium infestans*. Tree height, as an index for growth, was dependent on the amount of energy available during the vegetation season, and therefore negatively correlated with both altitude above sea level and wind velocity, and positively with global radiation.

In the severe winter of 1951-52 avalanches caused major destruction all over the Alps. This initiated a multidisciplinary research program to restore the upper treeline. The aim of the program was to develop methods to afforest treeless avalanche catchments and abandoned meadows within the subalpine forest belt in order to establish new protection forests.

Protection forests are an important feature in alpine landscapes. Many areas can only be permanently inhabited as long as these forests remain intact. In some of these forests, however, severe problems concerning stand stability have become evident. Inadequate plantation techniques in the past have frequently led to forests that were highly susceptible to natural hazards such as storms. On the other hand, locally dense ungulate populations prevented successful natural rejuvenation in the existing forests.

Both natural regeneration and artificial afforestation generally have become more difficult toward the alpine timberline, since all biological processes become slower with increasing altitude above sea level. In general, compared to natural invasion of forest trees, planting reduces the time needed to establish forests that fulfill their protective function. Therefore artificial afforestation may be highly desirable. Poor financial resources, however, may limit planting to the most promising sites.

The experimental afforestation at Stillberg was designed to obtain information about site conditions that determine success or failure of future afforestations, and to be able

to inform forestry personnel which sites would be most promising for successful planting and on which sites planting would be fruitless.

Cembran pine (*Pinus cembra* L.) is one of the three timberline species tested at Stillberg. This species, extending to the highest altitudes of any trees in the Alps, played an important role in the culture of local human populations (Holtmeier, these proceedings), produces valuable timber, and is esteemed by "green" tourism as an important feature of natural landscapes. Nonsustainable exploitation in medieval times and pastoralism reduced cembran pine to a fraction of its original abundance, although there is evidence for natural range expansion in the past 100 years. Artificial reproduction and establishment of cembran pine, on the other hand, pose many problems for practical forestry (Frehner and Schönenberger, these proceedings).

MATERIAL AND METHODS

The present study was conducted at Stillberg experimental area, a highly structured northeast slope (fig. 1) in the Dischma Valley near Davos, Switzerland (lat. 34°08' S., long. 171°41' E.). The area extends over 9.9 ha between 2,080 and 2,230 m above sea level. The highest parts reach beyond the altitudinal timberline. Before plantation in 1975 various site aspects like slope, exposure, global radiation (Turner 1966), wind conditions (Nägeli 1971), date of disappearance of snow cover in spring (Rychetnik 1987), number of snow-free days in winter, avalanche frequencies, soil types (Blaser 1980), and vegetation (mainly dwarf shrub communities) (Kuoeh 1970) were recorded on a very fine scale. Schönenberger (1975) described the site in detail. Results from the Stillberg experimental afforestation were published by Schönenberger and others (1988). Practical aspects for high-altitude forestry were included in Schönenberger and others (1990).

Three coniferous tree species were planted in 1975: 5-year-old cembran pines, 3-year-old mountain pines (*P. uncinata* (Miller) Domin = *Pinus montana* Miller = *Pinus mugo* Turra ssp. *uncinata* Domin) the erect form of the mugo pine, and 1-year-old European larches (*Larix decidua* Miller). Before planting, the whole area was divided into square units of 3.5 by 3.5 m (fig. 1). In each square unit 25 trees of one species were planted. The number of trees per unit may have been reduced by adverse local soil conditions like barren rock. The squares contained alternatively cembran pines, mountain pines, and larches. Altogether some 90,000 trees were planted in 4,052 square units.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Josef Senn, Walter Schönenberger, and Ueli Wasem are members of the High Altitude Afforestation Group at the Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland.

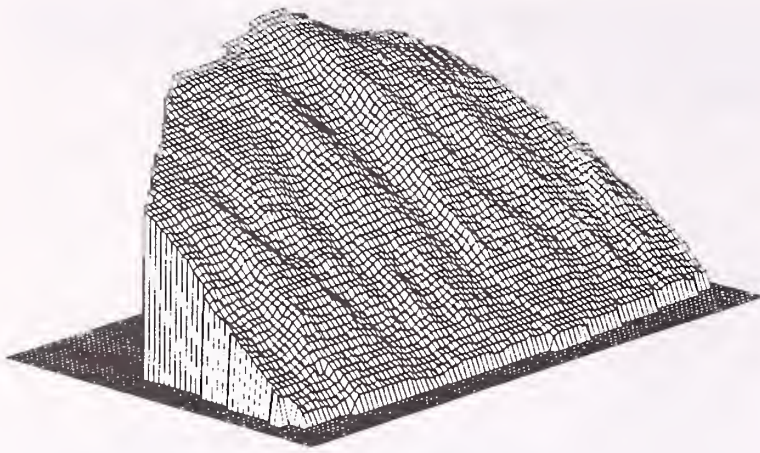


Figure 1—Topographic model of the Stillberg experimental area with the grid of the afforestation units (3.5 by 3.5 m).

This paper reports the results of survival of the cembran pines in comparison with mountain pine and European larch in the whole study area, and of height variation and mortality causes in a subsample. Survival of each tree was recorded annually as from 1976 (number of square units with cembran pines = 1,351, with mountain pines = 1,350, and with larches = 1,351). Mean tree height, general constitution, type and degree of abiotic and biotic damage, and causes of mortality were determined annually in 228 square units containing cembran pines, in 226 square units containing mountain pines, and in 226 square units containing larches. Twenty-eight qualitative “types” of damage and potential causes of death could be attributed in the field.

Correlation analysis was used to test for interactions between various site parameters and tree performance. The relative importance of site parameters was evaluated by stepwise regression analyses (SAS 1985) for survival and tree height. The survival rates were arcsine transformed before performing stepwise regression analysis.

RESULTS

Survival

During the first 3 years after planting, survival was highest in cembran pine compared to mountain pine and larch, but in 1991 only 25.3 percent of the planted cembran pines survived, compared to 37.8 percent in mountain pine and 73.1 percent in larch (fig. 2).

Stepwise regression of survival rate in a square unit (number of trees alive in 1991/number of trees planted in 1975) of cembran pine revealed that the date of disappearance of snow cover in spring and the altitude above sea level were the most important factors, explaining some 46 percent and 8 percent of total variation, respectively. In our study area the survival rate was high on the early snow-free and lower sites. Survival decreased with increasing altitude, and almost no trees survived on sites where snow lasted on 10-year average longer than June 10.

Avalanche frequency, slope inclination, global radiation, and the number of snow-free days in winter also had significant effects on survival, but each of these factors contributed less than 1 percent to the total variation.

Mortality Causes

Of the 28 recorded causes for mortality, *Ascocalyx abietina* (Lagerb.) (= *Gremmeniella abietina* [Lagerb.] Morelet), a parasitic fungus, was the major factor, killing some 52.3 percent of the planted cembran pines. A second fungus, *Phacidium infestans* Karst., the snow blight, killed another 11.8 percent of the trees. Some 4.8 percent of the trees died or disappeared without any detectable reason. Undetermined fungi killed 1.3 percent and competition with herbaceous vegetation some 0.6 percent of the planted trees. Herbivores caused no losses.

We found a significantly positive correlation between the proportion of cembran pines killed by *Ascocalyx abietina* and the date of disappearance of snow cover in spring (fig. 3). Square units that were snow free before May 12 suffered only slightly (13.9 percent of the trees killed), whereas *Ascocalyx* killed 90.3 percent of the trees in units that were covered by snow later than June 10. Occurrence of *Ascocalyx* was also positively correlated with altitude ($r = 0.55$, $P < 0.0001$, $n = 228$), the fungus killing an increasing proportion of young trees with increasing altitude.

Between the proportion of cembran pines killed by *Phacidium infestans* and the date of disappearance of snow cover in spring, however, we found a negative correlation ($r = -0.42$, $P < 0.001$, $n = 228$). This means that the highest proportion of trees was killed in squares that were

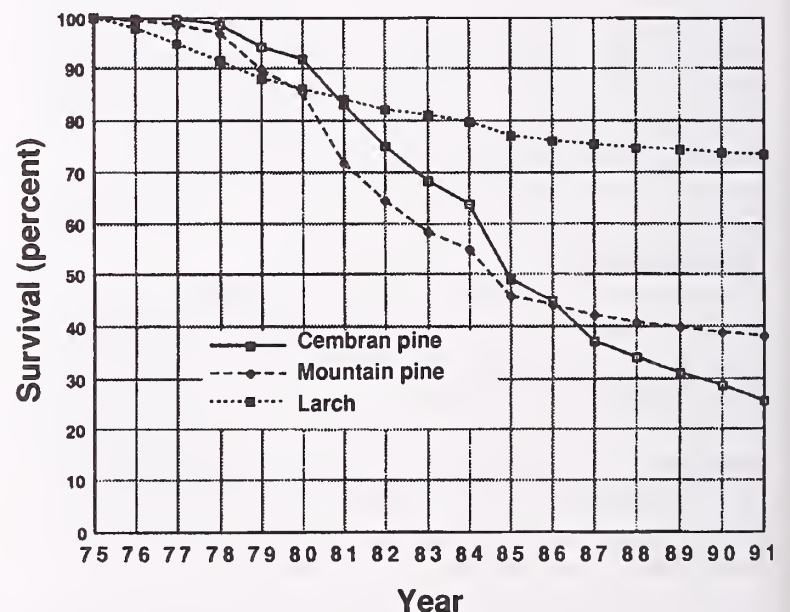


Figure 2—Survivorship curves of the three tree species, cembran pine (*Pinus cembra*), mountain pine (*P. uncinata*), and European larch (*Larix decidua*), planted in 1975 in the Stillberg experimental area.

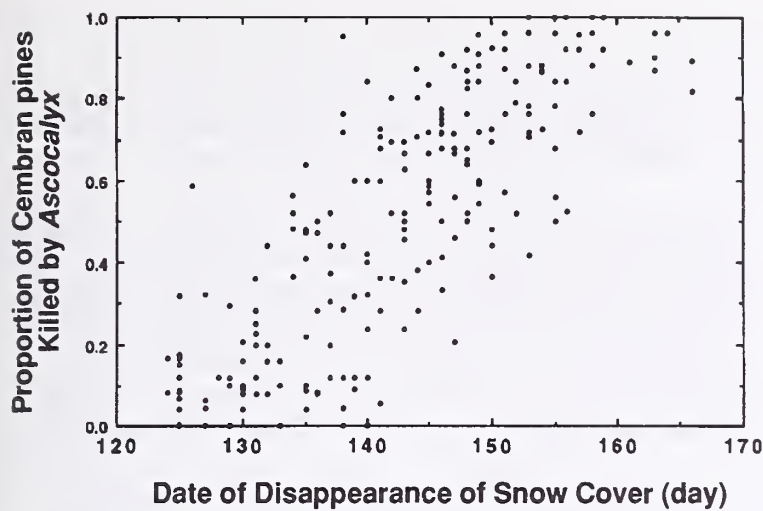


Figure 3—Relationship between the proportion of cembran pines killed in a square unit by *Ascocalyx abietina* (= number of trees killed by *Ascocalyx* since 1976/number of trees planted in 1975) and the date of disappearance of snow cover in spring. Day 130 = May 10; day 160 = June 9. Regression line: $y = -3.0637 + 0.0251x$, $r = 0.81$, $P < 0.0001$, $n = 228$.

snow free early, whereas the importance of *Phacidium* as a mortality cause decreased with increasing duration of snow cover. Similarly the ratio of trees killed by *Phacidium* decreased with increasing altitude ($r = -0.26$, $P < 0.0001$, $n = 228$).

The occurrences of the two parasitic fungi were significantly negatively correlated within square units ($r = -0.59$, $P < 0.0001$, $n = 228$). If one of the two fungus species was common in one square, the other was rare.

Tree Height

Mean tree height in 1991 was lowest in cembran pine (58.8 cm) compared to mountain pine (72.7 cm) and larch (59.8 cm), although initial mean height was largest in cembran pine (fig. 4).

Variation in height was considerable, depending on local site conditions. On sunny southeast exposed sites, average height of cembran pines was above 80 cm, whereas on shady sites mean height was around 45 cm. Stepwise regression revealed that tree height was mainly affected by altitude, global radiation, and wind velocity, these factors contributing 21 percent, 15 percent, and 10 percent to the total variation. Duration of snow cover in spring explained 3 percent of the variation in height. In our study area the cembran pines were high on sites at low altitudes, receiving high amounts of radiation and being protected from strong winds. Slope inclination, avalanche frequency, and number of snow-free days in winter had no significant impact on tree height.

DISCUSSION

Survival

Duration of snow cover in spring was found to be the main limiting factor for survival of young cembran pines in the upper subalpine forest belt. On sites where snow cover lasted until after June 10 cembran pines were almost completely excluded. The second evergreen *Pinus* species, the mountain pine, was similarly vulnerable to long-lasting snow cover. The European larch, a deciduous conifer, was much more tolerant. In this species 30 percent of the trees survived on sites snow covered until after June 10. Further, survival of cembran pine was significantly affected by altitude, although this factor was clearly less important than duration of snow cover in spring. Interestingly, the impact of site factors such as global radiation, number of snow-free days, slope inclination, and avalanche frequency on tree survival was negligible compared to the first two factors. Avalanche frequency, however, will certainly become more important in the near future. Young trees with flexible stems generally survive avalanche impacts without significant damage. But with increasing height and stem diameter the trees are becoming increasingly vulnerable to stem breakage caused by snow movements, a tendency that has become evident only during the last years.

Mortality Causes

In our study area the two parasitic fungi *Ascocalyx abietina* and *Phacidium infestans* were the major mortality factors for cembran pines, and these fungi still kill significant numbers of young trees every year.

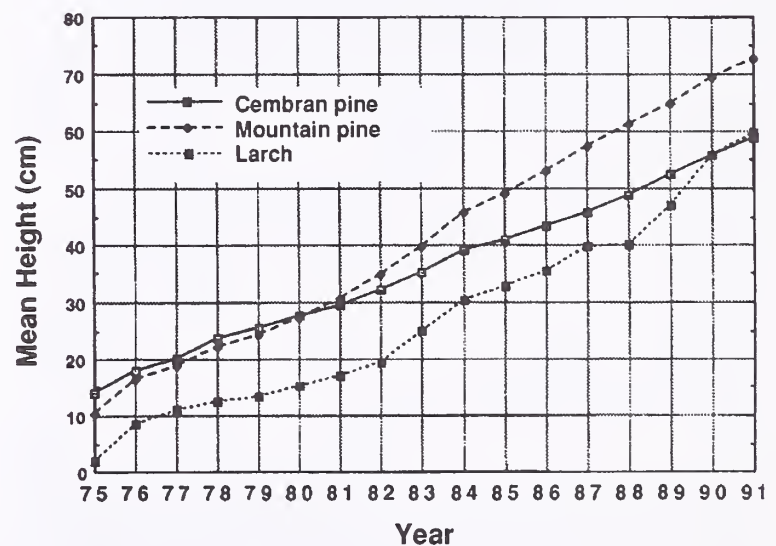


Figure 4—Annual mean height of the three tree species, cembran pine (*Pinus cembra*), mountain pine (*P. uncinata*), and European larch (*Larix decidua*), planted in 1975 in the Stillberg experimental area.

Ascocalyx infestations first become evident in spring in the dying buds. Later in the season the shoots die back along the branches. The fungus may eventually kill a young cembran pine after 2 or 3 years. The close relationship between the date of disappearance of snow cover in spring and the occurrence of *Ascocalyx* (fig. 3) indicates that the fungus preferentially attacks weakened plants. On the sites with long-lasting snow cover, the vegetation season is relatively short, and thick layers of raw humus have accumulated because of the low temperatures. Therefore, they are poor sites for tree growth. Similarly, Kurkela (1984) found that the trees most heavily affected by *Ascocalyx* had the lowest growth rate before the epidemic. He explained the differences in tree growth by the different site fertility. In our study the hypothesis that *Ascocalyx* preferentially attacked weakened trees was further supported by the finding that the proportion of trees killed by the fungus significantly increased with increasing altitude (toward the altitudinal tree line). In our study area *Ascocalyx* attacked mountain pines, too, where it also caused considerable losses.

In contrast to the situation in *Ascocalyx*, the proportion of cembran pines killed by *Phacidium* was negatively correlated with the date of disappearance of snow cover and with the altitude. According to this correlation the trees growing at lower altitudes and on sites that were snow free early were killed more frequently by *Phacidium* than the trees growing at higher altitudes and on sites with long-lasting snow cover. Young trees that looked healthy in one year were often found dead in the following spring. Interestingly, Roll-Hansen and others (1992) reported from Scandinavia that the most vigorously growing plants were most susceptible to *Phacidium* infestations, whereas poorly developing plants were most resistant.

The fact that *Phacidium* killed the highest proportion of trees at early snow-free sites seems contradictory to the biology of the fungus, that exclusively attacks parts of trees that are covered by snow (Roll-Hansen 1989). Branches destroyed by this fungus are clearly visible after disappearance of snow cover and mark the prevalent snow depth. Our study area contains some older cembran pines growing on ridges (at the sites that are snow free early). These trees originating from caches of the nutcracker (*Nucifraga caryocatactes*) host *Phacidium*, which is non-lethal for the large trees that extend considerably beyond the snow cover. These trees may act as sources for local *Phacidium* outbreaks that eventually kill the young trees completely covered by snow. Since this fungus specifically attacks cembran pine and does not occur on mountain pine (but see Roll-Hansen 1989), it may not spread as easily over larger areas as does *Ascocalyx*, which uses mountain pine as an alternative host. Therefore, even heavier outbreaks of *Phacidium* remain locally restricted around mature cembran pines. Together with the fact that *Phacidium* preferentially attacks the most vigorous trees, this may explain the seemingly paradoxical negative correlation between duration of snow cover in spring and occurrence of *Phacidium*.

On sites with high avalanche frequencies the young trees were partially excluded, not by stem breakage or uprooting, but by competitive interactions with herbaceous vegetation. The moving snow carried rich mineral

soil leading to a lush herbaceous vegetation that out-competed the slowly growing young cembran pines. Avalanches, however, become a more serious problem for the surviving trees as they increase in height and stem diameter. Broken stems were found more frequently in recent years.

Herbivore impact on the survival of young cembran pines was relatively unimportant. Herbivores killed no trees, although they may reduce tree growth. Browsing vertebrates like black grouse (*Tetrao tetrix*) and chamois (*Rupicapra rupicapra*), however, clearly preferred mountain pine and larch to cembran pine. Black grouse caused some locally restricted damage by browsing buds and first-year needles. They obviously preferred to browse on easily accessible trees growing on ridges with little snow cover (Streule 1973). Populations of herbivorous insects like phloem-sucking aphids (*Cinara cembrae* Seitner, see Grbic, these proceedings, and *Pineus cembrae* [Chol.] Amand.) fluctuated in size but were low in most of the years when compared to the other two tree species. Although visible damage by herbivores was relatively rare, much rarer than fungal infections, the herbivores may have indirectly affected the survival of the trees by injuring plant tissue, making the trees more susceptible to infestations by fungi.

Tree Height

Tree height in cembran pine was clearly dependent on the available amount of energy during the vegetation season. Altitude above sea level, global radiation, and wind velocity explained the largest amount of variation in height. We are aware that tree height does not directly represent tree growth, since we did not measure annual growth. We only recorded tree height in summer, excluding the growing shoot of the current year. Tree height, which is the result of annual growth minus the losses through damage in the apical region, may increase or decrease from one year to another. Sixteen years after plantation, differences in average tree height among sites, however, are primarily the result of variation in growth caused by variation in local site conditions.

The date of disappearance of snow cover in spring, although significantly related to tree height, explained only 3 percent of the variation in height in contrast to survival where the snow conditions in spring mainly explained the observed pattern.

Slope inclination and avalanche frequency, which may be related to stem breakage, had no detectable impact on tree height. Further, we found no relationship between the number of snow-free days in winter and tree height, although trees that were snow free during extended periods in winter should have been more vulnerable to herbivore browsing than trees that were covered by deep snow.

CONCLUSIONS

Foresters should carefully select favorable microsites when planting cembran pines in high-altitude afforestations. Particular attention should be paid to the spatial pattern of snowmelt in spring, and no cembran pines should be planted at sites with prolonged duration of snow cover.

REFERENCES

- Blaser, P. 1980. Der Boden als Standortsfaktor bei Aufforstungen in der subalpinen Stufe (Stillberg, Davos). Eidgenössische Anstalt für das forstliche Versuchswesen, Mitteilungen. 56(3): 527-611.
- Kuoch, R. 1970. Die Vegetation auf Stillberg (Dischmatal, Kt. Graubünden). Eidgenössische Anstalt für das forstliche Versuchswesen, Mitteilungen. 46(4): 329-342.
- Kurkela, T. 1984. The growth of trees affected by *Gremmeniella abietina*. In: Manion, P. D., ed. Sclerodermis canker of conifers. The Hague: Martinus Nijhoff/Dr W. Junk Publishers: 177-180.
- Nägeli, W. 1971. Der Wind als Standortsfaktor bei Aufforstungen in der subalpinen Stufe (Stillbergalp im Dischmatal, Kanton Graubünden). Eidgenössische Anstalt für das forstliche Versuchswesen, Mitteilungen. 47(2): 33-147.
- Roll-Hansen, F. 1989. *Phacidium infestans*: a literature review. European Journal of Forest Pathology. 19: 237-250.
- Roll-Hansen, F.; Roll-Hansen, H.; Skröppa, T. 1992. *Gremmeniella abietina*, *Phacidium infestans*, and other causes of damage in alpine, young pine plantations in Norway. European Journal of Forest Pathology. 22: 77-94.
- Rychetnik, J. 1987. Snow cover disappearance as influenced by site conditions, snow distribution, and avalanche activity. In: Proceedings of the international symposium on avalanche formation, movement and effects; Davos 1986. IAHS-Publication Nr. 162.
- SAS. 1985. SAS user's guide: statistics. Cary, NC: SAS Institute.
- Schönenberger, W. 1975. Standorteinflüsse auf Versuchsaufforstungen an der alpinen Waldgrenze (Stillberg, Davos). Eidgenössische Anstalt für das forstliche Versuchswesen, Mitteilungen. 51(4): 357-428.
- Schönenberger, W. 1985. Performance of a high altitude afforestation under various site conditions. In: Turner, H.; Tranquillini, W., eds. Establishment and tending of subalpine forest: research and management: Proceedings of the 3rd IUFRO workshop P 1.07-00, 1984. Eidgenössische Anstalt für das forstliche Versuchswesen, Berichte. 270: 233-240.
- Schönenberger, W.; Frey, W., eds. 1988. Untersuchungen zur Ökologie und Technik der Hochlagenaufforstung; Forschungsergebnisse aus dem Lawinenanrissgebiet Stillberg. Schweizerische Zeitschrift für Forstwesen. 139: 735-820.
- Schönenberger, W.; Frey, W.; Leuenberger, F. 1990. Ökologie und Technik der Aufforstung im Gebirge - Anregungen für die Praxis. Eidgenössische Anstalt für das forstliche Versuchswesen, Berichte Nr. 325. 58 p. [Version française: Ecologie et technique des afforestations en montagne - Suggestions à l'usage des praticiens. Traduction du rapport No. 325.] [Versione italiana: Ecologia del rimboschimento di montagna e pratica della tecnica di piantagione. Traduzione del rapporto No. 325.]
- Streule, A. 1973. Schäden in Gebirgsaufforstungen durch das Birkhuhn (*Lyrurus tetrix*). Bündnerwald. 28(8): 249-254.
- Turner, H. 1966. Die globale Hangbestrahlung als Standortsfaktor in der subalpinen Stufe. Eidgenössische Anstalt für das forstliche Versuchswesen, Mitteilungen. 42(3): 111-168.

Influence of Environmental Factors



International Workshop
St. Moritz 1992

CHANGES OF SWISS STONE PINE APHID LIFE CYCLE, DENSITY, AND POPULATION STRUCTURE IN HIGH- ALTITUDE SWISS STONE PINE AFFORESTATION

Mihailo Grbic

Abstract—The order of form appearance, structure, and number of individuals in colonies of *Cinara cembrae* on Swiss stone pine (*Pinus cembra*) used for afforestation in the Dischma Valley were strongly related to the slope aspect. The abnormality was particularly apparent on north slopes. North slope colonies showed incomplete life cycles. All insects seen there were virginoparae and their larvae. Colonies were small in number and were developed from winged virginoparae from other areas.

The Alps are of great importance to Switzerland as an area for human habitation and as a health and holiday resort. Afforestation in high altitudes is costly and involves high risk, as many failures occur. Because of the slow development of such afforestation it is difficult to understand and to determine the causes and processes that lead to a failure and then to suggest measures to improve success.

Environmental factors of the upper timberline area are totally different from those of the forest zones. These harsh conditions affect the specific growth and development of planted species; for example, low survival rate and low annual increment. The surviving plants, depending on the biological characteristics of the species, are more or less open to insect and fungal attack. These same high-altitude factors (for example, low temperature, short growing period, and short day photoperiod) tend to change the life cycle, density, and population structure of insects. This is particularly true for aphids due to their polymorphic nature, and their ability to alter the number of generations per season.

STUDY AREAS AND METHODS

These investigations were carried out in field plots of the Stillberg research area and the Lucksalp comparative afforestation area, in the timberline area of the Dischma Valley (Canton Graubunden). The period of the study was between late May and the middle of September, which is the time of greatest insect activity.

Stillberg lies at 2,080 to 2,230 m above sea level (a.s.l.), with a northeast aspect, and 30° to 45° slope. The slope is divided by spurs, and as a result there are three different aspects (north-, northeast-, and east-facing slopes). On the opposite side of Dischma Valley lies Lucksalp at 2,200 m a.s.l., with a southwest aspect.

The subjects of investigation were 19-year-old Swiss stone pine (*Pinus cembra* L.) and the Swiss stone pine aphid (*Cinara cembrae* Seithner), the most frequently observed insect pest on that afforestation species. The trees were planted 70 cm apart in a grid pattern in approximately 4,000 square plots (3.5 by 3.5 m). The Swiss stone pine stocks were alternated from plot to plot with two other afforestation species, 17-year-old Swiss mountain pine (*Pinus mugo* ssp. *uncinata* [Mill.] Domin.), and 15-year-old European larch (*Larix decidua* Mill.), each plot containing 25 trees (Shönenberger 1985).

The samples of Swiss stone pine aphid were identified by comparing them to recent accounts from various parts of Europe (Carter and Maslen 1982; Eastop 1972; Pintera 1966; Stroyan 1955, 1960). The structure of antennae, rostrum, abdomen, and hind legs of collected material were compared with these references.

The life cycle was observed in colonies feeding on particular sample trees. On Lucksalp, 30 trees (5 trees x 6 plots) were regularly examined, and 50 (5 trees x 10 plots) were examined on Stillberg. Observations were made to establish the relationship between the intensity of infestation and site aspects.

The trees were examined every 10 days to determine density of pest population and structure of colonies.

MORPHOLOGY

The morphological characteristics of specimens found on Stillberg and Lucksalp (tables 1 and 2) are similar to the central European description (Pintera 1966). The chronological series of morphs is: fundatrix, aptera virginopara, alata virginopara, ovipara, and aptera and alata males.

Compared with the apterae of the succeeding generations, fundatrix shows "fundatrix facies" characteristics (Lees 1961). With the Swiss stone pine aphid, the antennae and legs are relatively shorter in comparison to the body. The processus terminalis is shorter with fewer rhinaria. Features similar to the fundatrix facies that were observed by Hille Ris Lambers (1955), Lees (1961), and Stroyan (1960) on nonfundatrix morphs of some

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Mihailo Grbic is Teacher at the University of Belgrade, Faculty of Forestry, Kneza Visislava 1, YU-11030 Belgrade, Yugoslavia.

Table 1—Biometric data for different morphs of *Cinara cembrae* from Lucksalp

Biometric data	Morph				
	Aptarae virginoparae	Alatae virginoparae	Aptarae male	Alatae male	Sexual female
Body length (mm)	3.05-3.52	3.00-3.10	2.50-3.30	2.40-3.00	3.80-4.70
Length of antennal segments (μ)					
II	680-720	635-650	830-880	845-910	830-890
IV	300-340	275-290	335-400	360-430	360-385
V	400-410	320-345	430-500	440-500	480-500
VI (base + proces. terminalis)	167-180 + 75-83	150-160 + 59-66	190-198 + 75-90	109-198 + 85-95	192-212 + 75-80
Length of rostral segments (μ)					
IV	218-238	170-182	230-250	220-230	245-250
V	100-112	85-88	90-110	105-110	106-118
Hind tarsus segments (μ)					
I					
basal diameter	74-78	57-62	60-70	60-65	68-88
dorsal length	95-105	62-66	98-110	85-105	105-120
ventral length	155-182	122-130	150-180	150-180	187-200
II					
length	385-420	330-350	340-390	385-400	370-420
Hind tibia length (mm)	3.20-3.30	2.90-3.05	1.85-3.00	2.90-3.40	3.70-3.78
Length of longest hair on					
III ant. segment	75-97	88-92	75-120	115-140	95-123
hind tibia	75-120	70-105	75-110	140-180	112-145
VIII abdom. tergite	110-165	185-200	100-112	90-120	120-138
Number of hairs on					
II ant. segment	9-15	6-7	10-15	7-14	10-16
VI ant. segment					
base	9-13	10-12	10-12	8-10	8-13
proces. term.	4-5	3-4	5	5-6	5-6
ultimate rostral segment	6-8	8	10-12	8-10	9-11
Number of hairs on					
subgenital plate	10-12	10	10-12	6-9	9-13
VIII abdom. tergite	4-6	—	7-11	6-9	7-8
Number of secondary rhinaria on					
ant. segments					
III	0-2	9-11	10-13	55-83	2-3
IV	0-2	2-3	7-10	10-13	1-2
VI	2-3	5	4-5	5	4-7

aphids that live at low temperatures were not recorded in these study areas.

Morphological differences between apterous and alatae virginoparae are found not only in the presence or absence of the wings, but also in the following characteristics. In alatae:

- Segmentation between head and prothorax is more conspicuous.
- Compound eyes are bigger, with many facets.
- Antennae bear five times as many rhinaria.
- The body is shorter, and the mesothoracic terga consists of a compound notum and postnotum.
- The scutum occupies the central major part of the notum and is divided in two mesothoracic lobes, which are hardly developed.

The virginoparae of every generation are morphologically uniform, and under field conditions it is impossible to find out how many generations have developed. Also, the length of time required for passing through four instars, from birth to adult, is variable and dependent on two external factors (food quality and temperature) and two internal factors (birth weight and whether the morph is winged or unwinged) (Dixon 1987). This is the reason for the presence of different generations of the same form occurring simultaneously in one colony.

As is known, Swiss stone pine aphids produce both alatae and apterous males. Both forms were found in the research areas, but with a preponderance of the wingless form. Both forms of males are readily recognized by their sclerotized genital structure. The body, especially abdomen, is smaller and more slender, and the antennae bear more rhinaria.

Table 2—Biometric data for different morphs of *Cinara cembrae* from Stillberg

Biometric data	Morph				
	Aptarae virginoparae	Alatea virginoparae	Apterae male	Alatae male	Sexual female
Body length (mm)	2.90-3.70	2.90-3.90	2.50-3.10	2.40-3.00	3.90-4.70
Length of antennal segments (μ)					
II	540-800	630-650	820-800	840-930	800-860
IV	260-355	250-280	320-400	360-440	350-400
V	340-450	330-360	430-500	450-510	470-500
VI (base + proces. terminalis)	170-188 + 80-85	153-167 + 58-68	183-210 + 75-95	192-200 + 88-95	175-222 + 75-85
Length of rostral segments (μ)					
IV	238-250	162-172	235-250	220-225	235-250
V	100-108	83-87	95-102	100-105	105-118
Hind tarsus segments (μ)					
I					
basal diameter	75-78	55-59	52-75	60-65	68-105
dorsal length	88-108	60-62	95-102	88-107	105-125
ventral length	158-175	122-127	150-178	150-170	185-230
II					
length	365-385	300-340	335-395	380-400	420-450
Hind tibia length (mm)	2.40-3.39	2.82-2.98	1.78-2.98	2.95-3.37	3.70-3.88
Length of longest hair on					
III ant. segment	60-88	85-88	78-125	112-142	95-130
hind tibia	60-105	75-110	78-112	140-175	112-150
VIII abdom. tergite	168-220	195-210	100-115	88-130	112-138
Number of hairs on					
II ant. segment	11-15	6-7	10-16	7-15	10-18
VI ant. segment					
base	8-12	9-13	10-13	8-11	8-16
proces. term.	4-5	3-4	5-6	5	4-6
ultimate rostral segment	8-9	7-9	9-12	8-11	8-11
Number of hairs on					
subgenital plate	9-11	6	9-12	6-9	9-14
VIII abdom. tergite	4-6	—	7-12	6-9	6-9
Number of secondary rhinaria on					
ant. segments					
III	0-4	8-10	10-15	50-89	2-4
IV	2-3	1-3	7-11	11-15	0-2
VI	3-4	6	4-6	5-6	2-7

Alatae and apterous males and alatae virginoparae possess a far larger number of secondary rhinaria than apterous virginoparae and sexuales females. The following numbers of secondary rhinaria on the third antennal segment were found: apterous virginoparae 0-4, alatae virginoparae 8-11, apterous males 10-15, and alatae males 50-89. The number of secondary rhinaria on sexuales females was similar to that found in apterous virginoparae.

The function of secondary rhinaria is probably different in male and female individuals. The secondary rhinaria in males appear to be the main receptors of sex pheromones, while secondary rhinaria of alatae virginoparae must have a function other than pheromone detection. This function is possibly host selection, as has been shown by many authors with other aphid species (Alikhan 1960; Chapman and others 1981; and Pospisil 1976).

Sexuales females resemble the apterous virginoparae, but may be somewhat bigger. The tibiae of the hind legs are often longer with longer setae also, and numerous pseudosensoria on them.

LIFE CYCLE

General—The life cycle of the Swiss stone pine aphid is strongly related to site aspects and environmental factors. Generally, the Swiss stone pine aphid has a monoecious holocyclic type of life cycle. The life cycle starts in May with the hatching of fundatrices larvae from eggs laid in rows on the needles. In the course of summer a small number of generations of parthenogenetic females develop.

Generations of winged parthenogenetic viviparous females arise from colonies of apterae later in the summer.

Sexuales forms appear in the second half of August. This early development of sexuales is due to the alpine climate. In the low-lying positions where Swiss stone pine has been artificially introduced, Swiss stone pine aphid has never been found.

Observed—The life cycle observations in the Dischma Valley show the following characteristics: colonies from Lucksalp and all slopes of Stillberg, except north-facing slopes, show complete life cycles with six morphs. Parallel appearance of two forms of males, observed by Seithner (1936), is a unique case in the family Lachnidae. The north-slope colonies showed incomplete life cycles. All insects seen there were virginoparae apterae or alatae and their larvae. Colonies were small in number and were developed from winged virginoparae from other areas that colonized plants on north-facing slopes from other areas (table 3).

The order of appearance of particular forms on Lucksalp was earlier than on the Stillberg research area. The first observation, made in the last third of May, shows 68 percent unhatched eggs, and all fundatrix larvae were part of the first two larval instars. At the same time on Stillberg 87 to 90 percent of the eggs were unhatched.

In the first third of June the colony structure on Lucksalp was: 7 percent of the eggs were unhatched, young fundatrices in all four larval instars were found, but no adults. A similar, but slightly different, situation was recorded on Stillberg. There were 25 to 38 percent unhatched eggs, and the colonies contained only the first three larval instars.

During the observations in the second third of June we found adult fundatrices on Lucksalp and on the east slopes of Stillberg. With the appearance of fundatrices, the density of populations increased gradually.

On the other Stillberg slopes (ENE and NE) fundatrices were found 10 days later. Simultaneously we recorded adults of apterous virginoparae on Lucksalp. This is a time of heavy increases in population, because the multiplication rate of apterous virginoparae is very high, and the duration of larval instars very short.

In an experiment that was conducted under conditions of changeable room temperature, one apterous virginoparae was isolated on a twig that was kept moist. Ten days later, we recorded six apterous virginoparae of a new generation (which started with larviposition); 16 in the fourth larval instar; and 18 larvae were in younger stadiums.

It was presumed that the effect of the multiplication rate is not the same in nonisolated field conditions, but on some trees the increments of population for 10 days increased by a factor of 10 or more. On the other hand, some other populations were substantially reduced by the action of parasites and predators.

In the first third of July at Lucksalp a typical population consisted of more than 170 individuals; almost all belonged to apterous virginoparae larvae (83 percent) or adult insects (15 percent). The rest (2 percent) were alatoid larvae of alatae virginoparae. The fundatrix generation was dead. At Stillberg, populations were smaller

with most of the population made up of larvae and adults of apterous virginoparae; however, fundatrices were also found to be present. The fourth larval instar of alatae virginoparae was recorded on the east slopes only. The proportion of alatoid larvae was 10 percent of the total number of the fourth larval instar.

The first Swiss stone pine aphid was recorded on the north slopes of Stillberg in the middle of July. Colonies were small and consisted of only a few adult alatae virginoparae and young larvae. Few of the colonies were without adults. The population structures of the other slopes were unchanged in content until the last third of August. Only the numbers of individuals were variable, depending on weather conditions.

The rapid decrease in number of individuals at the beginning of August was caused by low temperatures and snow. The greatest changes in population quantity were recorded on north slopes. The average population structure in the course of July and August was: The majority of individuals belonged to various larval instars, and the adult part of the population consisted of apterae and alatae viviparous parthenogenetic females. Average ratio of winged and wingless forms was 1:5.3 with an increasing tendency to winged forms in colder sites. This tendency is due to the strategy of the species to avoid exposure to more extreme climatic conditions (by colonizing another host plant of the same species, but in better environmental conditions). Extremes of the ratio were 1:8 and 1:2. The first was recorded on Lucksalp, and the second on Stillberg north slopes.

The highest population numbers were found in the last third of July, after which the numbers decreased rapidly as a consequence of low temperatures at the beginning of August. Thereafter, the population number increased quickly again to a secondary peak at the end of August. Occurrence of the last generation was recorded after another cool weather period at the end of August. As the overwintering eggs are produced sexually, the last generation of the year must contain males and sexual females, instead of the parthenogenetic forms that occur during the rest of the year. However, sexuales do not occur under all investigated conditions. On the north slopes of Stillberg, for example, no sexuales forms were recorded. On Lucksalp, occurrence of sexuales forms was about 10 days before Stillberg.

The first appearance of eggs was observed at the beginning of September. Oviparous females move away from the colony to the top part of current shoots, and lay overwintering eggs in rows on needle clusters. Eggs were brown and later black and shiny 48 hours after being laid. Average number of eggs in the row along one needle was 8.2 and the extremes were 16 and 1. Maximum egg number per one colony was 316, recorded in the first week of September at Lucksalp. The same colony contained eight sexuales females. Results of dissection of females show 12 ripe eggs in the ovariole on average. This was smaller in comparison with the embryo numbers obtained by dissection of parthenogenetic females during July, which was 30.

Table 3—Average number of different morphs of *Cinara cembrae* on Swiss stone pine sample trees from last third of May to second third of September

Morph	May	June			July			August			September	
	3/3	1/3	2/3	3/3	1/3	2/3	3/3	1/3	2/3	3/3	1/3	2/3
Lucksalp (SW slope)												
Eggs	5.6	0.6									60.0	93.0
Larvae	2.6	7.6	35.0	103.0	148.0	178.0	199.0	68.0	82.0	124.0	9.0	11.0
Fundatrices			1.2	1.5								
Apterae virginoparae				2.0	27.0	12.0	24.0	8.3	18.0	24.0	7.3	6.7
Alatae virginoparae						1.5	2.4	1.8	1.5	2.0	0.2	
Oviparous females										0.1	4.9	5.4
Apterae males										0.1	0.3	1.4
Alatae males											0.1	
Stillberg (E slope)												
Eggs	7.2	2.0	0.2								3.8	57.0
Larvae	0.8	4.4	30.0	41.0	58.0	100.0	110.0	54.0	80.0	104.0	5.9	8.1
Fundatrices			0.6	1.8	1.0							
Apterae virginoparae					3.6	30.0	31.0	6.3	11.0	20.0	2.9	3.2
Alatae virginoparae							3.0		5.0	5.8		0.7
Oviparous females											0.2	2.3
Apterae males											0.1	0.3
Alatae males											0.1	0.2
Stillberg (ENE slope)												
Eggs	7.0	3.0	1.1									
Larvae	0.8	4.8	6.7	34.0	124.0	140.0	145.0	54.0	69.0	93.0	4.6	8.3
Fundatrices				2.4	0.2							
Apterae virginoparae					5.0	12.0	18.0	3.2	10.0	17.0	3.0	3.5
Alatae virginoparae							2.6	1.0	3.8	4.7	1.8	
Oviparous females											1.4	5.2
Apterae males											0.8	
Alatae males											0.2	0.5
Stillberg (NE slope)												
Eggs	6.5	2.0										8.0
Larvae	1.0	5.9	7.7	32.0	40.0	89.0	118.0	26.0	40.0	58.0	8.6	12.0
Fundatrices				2.3	0.8							
Apterae virginoparae					1.8	10.0	18.0	2.3	7.1	9.4	3.8	9.2
Alatae virginoparae							0.9	1.0	1.3	3.0	2.6	2.8
Oviparous females											0.8	2.0
Apterae males											0.7	1.5
Alatae males												
Stillberg (N slope)												
Eggs												
Larvae						5.8	43.0	1.0	11.0	18.0		
Fundatrices												
Apterae virginoparae							6.2	1.0	2.0	4.8		
Alatae virginoparae						1.0	3.4		1.6	1.2		
Oviparous females												
Apterae males												
Alatae males												

SEASONAL MOVEMENTS

The most important factors affecting aphid feeding and nutrition are the change, in time, of growth and development of the host plant (Klungauf 1987). In conjunction with this change, seasonal movements of colonies were observed.

The fundatrix generation moves from the needles where overwintering eggs were laid. Feeding sites of fundatrices, and later generations of virginoparae, in the course of June and first half of July were on last year's shoots. During July, colonies moved to twigs and branches in lower parts of the crown (in extreme cases some of the colonies were found on stems). This was just after the peak of the annual increment of the shoots, when they start to become lignified. It seems to be related to descending sap movement. Conifer lachnids, as phloem feeders, exploit food sources in lower parts of the plant that become available as the season progresses.

The alataid larvae of alatae virginoparae usually move from the colony to the tops of the shoots before their final moult. Here they moult into alatae adults and fly off to colonize similar positions on other plants.

Simultaneously with the occurrence of sexuales, the colonies moved ascendentally. At the end of the season the majority of the individuals were on last year's and current season's shoots. From this position oviparous females moved to lay eggs on needles.

Additional trials were carried out with colonies isolated by polytene covers, which prevented migration from top to bottom parts of the host plant. In the beginning, the density of isolated colonies was much higher than the density of nearby nonisolated colonies. However, early occurrence of alatae forms indicated an attempt to change the colonies' position.

Later, complete starvation of the population was caused by restriction of movement. It was concluded that the life cycle of Swiss stone pine aphid is very much synchronized with the growth and development characteristics of their host plant, and in conjunction with this, quality of nutrition.

PEST DAMAGES

Keen (1938) reported that several species of lachnids cause considerable injury to conifers in North America. Furniss and Carolin (1977) described visible signs of injury, such as yellowing of needles or reduction of growth of young trees. According to Seithner (1936), the damage to Swiss stone pine is quite unimportant, but he believed that the trees could be weakened by the sucking and that secondary pests (for example, *Pissodes* and *Pityophthorus*) could easily attack them.

We found no direct visible signs of damage by Swiss stone pine aphid except for some discolorations on feeding sites. Our observations show that retardation of the growth increment by Swiss stone pine aphid, if any, is much less significant than retardation due to other environmental factors.

Indirectly, Swiss stone pine aphid's honeydew excretion, in the absence of heavy rain, accumulates on the surface of the shoots and forms an ideal substrate for

saprophytic sooty mould fungi to develop. A black covering of hyphae and spores can reduce the quality of trees that are grown in parks, but for the Stillberg and Lucksalp research areas it is not so important. On the other hand, honey derived from honeydew, particularly from conifer lachnids, is highly valued and of considerable economic significance. Fossel (1971) found that the Swiss stone pine aphid produced copious honeydew in the mountainous districts of Austria.

CONCLUSIONS

Information gathered during this study has allowed the following conclusions to be drawn:

- Swiss stone pine aphid was the most common insect pest on Swiss stone pine used for afforestation in the research areas of the Dischma Valley.
- The morphological characteristics of specimens and the chronological series of morphs found on Stillberg and Lucksalp are similar to the conventional descriptions. However, for some site aspects of the Dischma Valley the life cycle of Swiss stone pine aphid was incomplete. The life cycle abnormality was observed on the north slopes of Stillberg.
- The order of appearance of particular insect forms, structure, and number of individuals in colonies also were strongly related to site aspects. This is particularly true for the temperature effect that caused later development and smaller sizes of colonies on the north slopes.
- Swiss stone pine aphid was observed to cause only unimportant discolorations on the feeding sites. The damage to the trees is much less significant than that produced by the normally harsh environmental conditions of the upper timberline area.

When looked at in isolation, the damage produced by the pest observed in this study cannot be considered serious. However, it is only one link in a chain of factors detrimental to the growth of afforestation plants. How the insect interacts with other factors harmful to tree growth (for example, fungi) is as yet unknown, and therefore the damage caused by colonies of Swiss stone pine aphid cannot be accurately assessed.

Until it is known how detrimental the aphid is, the importance of control measures or predators and parasites also cannot be estimated.

Clearly, 6 months investigation is too short for conclusive results. However, the information gained has provided an important first step in understanding the relationship between the insect pest, Swiss stone pine aphid, and the host plant, Swiss stone pine, in high-altitude afforestation.

REFERENCES

- Alikhan, M. A. 1960. The experimental study of chemotactic basis of host specificity in a phytophagous insect, *Aphis fabae* Scop. (Aphididae: Homoptera). *Annales Univ. Mariae Curie - Skłodowska, Sectio C.* 15: 117-158.
- Carter, C. I.; Maslen, N. R. 1982. Conifer lachnids in Britain. Alice Holt Lodge, Farnham, Surrey, England: Forestry Commission Research Station.

- Chapman, R. F.; Bernays, E. A.; Simpson, S. J. 1981. Attraction and repulsion of the aphid, *Cavariella aegopodii*, by plant odors. *Journal of Chemical Ecology*. 7: 881-888.
- Dixon, A. F. G. 1987. Parthenogenetic reproduction and the rate of increase in aphids. In: *Aphids: their biology, natural enemies, and control*. 2A: 269-287.
- Eastop, V. F. 1972. A taxonomic review of the species of *Cinara* Curtis occurring in Britain (Hemiptera: Aphididae). *Bulletin of the British Museum, Natural History (Entomology)*. 27: 103-186.
- Fossel, A. 1971. New observation on *Cinara cembrae* (Homoptera, Lachnidae). *Annales Zoologici*. 28: 353-365.
- Furniss, R. L.; Carolin, V. M. 1977. Western forest insects. Misc. Publ. 1339. Washington, DC: U.S. Department of Agriculture, Forest Service. 654 p.
- Hille Ris Lambers, D. 1955. Hemiptera 2. Aphididae. *Zoology of Iceland*. 3(52a): 1-29.
- Keen, F. P. 1938. Insect enemies of western forests. Misc. Publ. 273. Washington, DC: U.S. Department of Agriculture.
- Klingauf, F. A. 1987. Feeding, adaptation and excretion. In: *Aphids: their biology, natural enemies, and control*. 2A: 225-253.
- Lees, A. D. 1961. Clonal polymorphism in aphids. In: *Insect polymorphism. Symposia of the Royal Entomological Society of London*. 1: 68-79.
- Pintera, A. 1966. Revision of the genus *Cinara* Curt. (Aphidodea, Lachnidae) in Middle Europe. *Acta ent. bohemoslov.* 63: 281-321.
- Pospisil, J. 1976. Sensory, olfactory and visual orientation of insects of the tropical region III. Visual and olfactory orientation of alate forms of the aphid, *Aphis gossypii* Glover, in Cuba. *Academia de Ciencias de Cuba, Serie Biologica*. 66: 17-23.
- Schönenberger, W. 1984. Performance of a high altitude afforestation under various site conditions. *Proc. 3d IUFRO Workshop*: 233-240.
- Seither, M. 1936. *Lachnus cembrae* an. sp., die Zirbenblattlaus. *Centralbl. ges. Forstwes.* 62: 33-49.
- Stroyan, H. L. G. 1955. Recent additions to the British aphid fauna. Part II. *Transactions of the Royal Entomological Society of London*. 106: 283-340.
- Stroyan, H. L. G. 1960. Three new subspecies of aphids from Iceland (Hem., Hom.). *Entomologiske Meddelelser*. 29: 250-265.

GENETIC CONSEQUENCES AND RESEARCH CHALLENGES OF BLISTER RUST IN WHITEBARK PINE FORESTS

Raymond J. Hoff
Susan K. Hagle
Richard G. Krebill

Abstract—Susceptibility of whitebark pine (*Pinus albicaulis*) to blister rust (caused by *Cronartium ribicola*) is reviewed. Progress is reported on studies that assess the level of susceptibility over its entire range and the existence of resistance in various stands. Two breeding approaches are discussed: (1) the traditional, where trees are selected, tested, then established in seed orchards; (2) a natural approach that aids natural processes to establish “a natural selection stand.”

In 1910, eastern white pine (*Pinus strobus*) seedlings that had been grown in Europe were planted in the area of Point Grey, BC, Canada. Some of these seedlings were infected with white pine blister rust (caused by the fungus *Cronartium ribicola*). The disease was finally noticed in the fall of 1921, when it was observed on endemic western white pine (*Pinus monticola*). The destructive nature of this disease in North American white pines had already been documented in Europe (Spaulding 1911).

What followed was a frantic rush to stop blister rust's spread by destroying infected trees, eradicating currants and gooseberries (genus *Ribes*) that are alternate hosts for the disease, and using several promising fungicides. But this work failed, and the fungus kept spreading. By about 1960, the fungus had spread throughout most the range of whitebark pine (*Pinus albicaulis*) (fig. 1), which also includes most of the range of western white pine and sugar pine (*Pinus lambertiana*). Examples of blister rust on whitebark pine are illustrated in figure 2.

The first infected whitebark pine recorded was in the arboretum of the University of British Columbia, Vancouver, BC, in 1922 (Bedwell and Childs 1943). The first discovery of blister rust on native whitebark pine was in 1926 on the Birkenhead River in the Coast Range of British Columbia, Canada (Childs and others 1938). Intense infection and mortality by blister rust was not far behind (Bedwell and Childs 1943).

The degree of infection was 100 percent in many stands in the northern areas, and decreased to the south where

whitebark pine occurs in higher and drier sites. Whitebark pines growing below about 45° N. lat. in Idaho and Montana have much less rust than whitebark of higher latitudes. However, in the Cascade-Sierra Nevada Mountains the rust has spread to about lat. 36°15' N., where it



Figure 1—Range map of whitebark pine showing areas of high, moderate, and little or no blister rust incidence.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Raymond J. Hoff is Research Plant Geneticist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Moscow, ID 83843, USA. Susan K. Hagle is Pathologist, Northern Region, Forest Service, U.S. Department of Agriculture, Missoula, MT 59807, USA. Richard G. Krebill is Assistant Station Director and Pathologist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Ogden, UT 84401, U.S.A.



Figure 2—Cankers of blister rust on whitebark pine.

has been especially devastating to western white pine and sugar pine. Whitebark pine too has been heavily impacted in most of these mountain ranges. But no infection was found on whitebark pine at Tioga Pass, Yosemite National Park, at about 39° N. lat. in 1992.

The relative susceptibility of the white pines to blister rust has been tested by several workers. Bingham (1972b) summarized these reports (table 1). All reports agreed that whitebark pine was most susceptible of the tested five-needled pines. Further work was done by Bedwell and Childs (1943) to compare the relative susceptibility of whitebark versus western white pine. These two pines grow adjacent for much of their ranges, with whitebark pine at the high-elevation sites and western white pine lower. They often are found on the same site in the overlap zone. Childs and Bedwell (1948) found that susceptibility (in terms of numbers of cankers and speed of tree mortality) of whitebark pine was several times that of western white pine. They concluded that this difference was due in part to (1) a higher susceptibility of current year whitebark pine needles and (2) longer needle retention of whitebark pine (5.3 years for whitebark and 3.8 years for western white pine).

Table 1—Comparison of susceptibility in white pines to blister rust by Bingham 1972a or b and a reshuffle by Hoff and others 1980

Species	Bingham 1972a or b	Hoff and others 1980
<i>Pinus armandii</i>	1	4
<i>P. cembra</i>	1	3
<i>P. aristata</i>	1	—
<i>P. wallichiana</i>	2	6
<i>P. koraiensis</i>	2	1
<i>P. peuce</i>	3	5
<i>P. sibirica</i>	4	2
<i>P. parviflora</i>	5	3
<i>P. strobiformis</i>	6	8
<i>P. strobus</i>	7	11
<i>P. flexilis</i>	8	10
<i>P. monticola</i>	9	4
<i>P. lambertiana</i>	10	9
<i>P. albicaulis</i>	11	7

Bingham (1983) found one western white pine in 10,000 that was free of blister rust. The possibility of finding disease-free whitebark pine trees seemed pretty slim.

Nonetheless, at sites in northern Idaho and western Montana where mortality is over 90 percent due to blister rust, we have found a few individuals with no or just a few cankers. Though they certainly are rare (fig. 3). This gives us hope that there are resistant trees that can be used to reestablish populations in these areas.

Hoff and others (1980) presented data indicating that three phenotypically resistant whitebark pine trees included in a species trial did indeed have resistance to blister rust. In this same study, resistant collections of western white pine and sugar pine were also included. This resulted in a reshuffle of the white pines for susceptibility to blister rust (table 1). In this comparison, whitebark pine moved up along with resistant western white pine and resistant sugar pine. However, these same species were tested in France by Delatour and Birot (1982), in Japan by Yokota (1983), and in Germany by Stephan (1985), and the resistance level of the collections of whitebark, western white, and sugar pine was much lower (tables 2, 3, 4). The only explanation is that there are different races of blister rust at these other test sites.

In spite of this bad news, our plans are to proceed to develop resistance in whitebark pine, including as many

genes for resistance as possible. If new races of the fungus appear, the new resistant varieties should have adequate flexibility to exhibit resistance to the new races. This seems justified, since high levels of resistance in western white pine and sugar pine are still being observed in blister rust resistance tests, even though several races of the fungus are evident.

ACTIVE WORK AND PRELIMINARY PROGRESS

Blister Rust Surveys of Stands, Clearcuts, and Burns—Our objectives are to determine the level of blister rust damage over the range of whitebark pine and to locate phenotypically resistant trees. As mentioned, the degree of damage is associated with latitude. Phenotypically resistant trees have been located in most stands where high mortality to blister rust has occurred. We also observed a relatively large amount of natural regeneration occurring in clearcuts and burns adjacent to stands of whitebark pine that have had high rust-caused mortality. Table 5 shows the number of trees per acre and the degree of infection by blister rust in four such stands. Natural regeneration of whitebark pine occurs from unused seed caches of Clark's nutcracker. The



Figure 3—Blister rust-resistant candidate trees at Gisborne Mountain (A) and Burke's Peak (B).

Table 2—Percent of rust-infected seedlings in bulk collections of white pine species (from Delatour and Birot 1982)

Geographic group	Species	Number of lots	Percent infected
European	<i>P. cembra</i>	12	0
	<i>P. peuce</i>	7	0-20
Asian	<i>P. sibirica</i>	2	0
	<i>P. parviflora</i>	3	0
	<i>P. koraiensis</i>	7	0-9
	<i>P. wallichiana</i>	10	7-67
	<i>P. armandii</i>	1	58
American	<i>P. aristata</i>	1	2
	<i>P. albicaulis</i>	5	40-100
	<i>P. flexilis</i>	17	0-100
	<i>P. strobiformis</i>	9	40-100
	<i>P. lambertiana</i>	5	64-96
	<i>P. strobus</i>	24	88-100
	<i>P. monticola</i>	5	94-100

abundance of regeneration was surprising. It immediately brought up questions: At what level of mortality will there not be enough seed available for caching by the nutcracker? If the seed did not come from the adjacent high-mortality stand, where did it come from?

Artificial Inoculation With Blister Rust—The objective is to determine the level and variety of mechanisms that impart resistance in phenotypically resistant trees and in stands that have had high mortality by blister

Table 3—Results of inoculation in France and Idaho. Percent of rust infection on "resistant" crosses of *P. lambertiana* and *P. monticola* from inoculation in France or Idaho (Delatour and Birot 1982)

Seed lot No. and cross	France mean	Idaho
----- Percent -----		
<i>P. lambertiana</i>		
41 C F ₁	99	55
41 B F ₁	98	57
41 A F ₁	52	25
<i>P. monticola</i>		
43 B F ₁	96	40
43 E F ₁	93	30
43 C F ₁	76	40
43 A F ₁	32	30
43 F F ₁	73	65
43 D F ₁	35	45
47 A F ₁	75	65
46 H F ₂	63	35
46 E F ₂	56	40
46 B F ₂	55	45
46 F F ₂	44	35
46 G F ₂	40	30
46 D F ₂	38	20
46 A F ₂	37	30
46 C F ₂	24	15

Table 4—Comparison of blister rust susceptibility of some white pines from Stephan (1985)

North America species	Percent infection	Eurasia species	Percent infection
<i>P. albicaulis</i>	97	<i>P. armandii</i>	0
<i>P. aristata</i>	66	<i>P. cembra</i>	0
<i>P. balfouriana</i>	90	<i>P. koraiensis</i>	23
<i>P. flexilis</i>	98	<i>P. morrisonicola</i>	40
<i>P. lambertiana</i>	197 (76)	<i>P. parviflora</i>	22
<i>P. monticola</i>	99	<i>P. peuce</i>	22
<i>P. strobiformis</i>	88	<i>P. pumila</i>	0
<i>P. strobus</i>	100	<i>P. sibirica</i>	17
		<i>P. wallichiana</i>	40

¹Two seedlots were tested; one was not as susceptible as the other.

rust. A trial test was inoculated in August 1991 using methods outlined by Bingham (1972a). This test included about 1,000 seedlings from 36 families from 10 populations. The inoculation was light; only 26 percent of the seedlings developed needle spots. However, there was considerable variation among populations (table 6). Even with the light inoculation, it was encouraging to observe several seedlings that had what we call "premature needle shed" (McDonald and Hoff 1970). This is a resistance mechanism in which needles with needle spots are shed from 9 to 12 months after inoculation and before the rust fungus has invaded the stem. This type of resistance has been observed in several white pine species (Hoff and others 1980). The seedlings were reinoculated in August 1992 and as of November 1, 1992, 87 percent had needle spots.

Adaptive Variation of Whitebark Pine—How far can we transfer seed and not cause maladaptation in the seedlings? The range of whitebark pine extends nearly 19 degrees of latitude and 20 degrees of longitude, and from 1,524 to 3,354 m. In addition, the species grows in various ecological situations. It can fill the role of a pioneer and a seral. It can exist for long periods as a dominant on harsh sites and even in some stands with the climax species, subalpine fir. Whitebark pine is found in 106 of 225 habitat/phase types in eastern Idaho-western Wyoming, central Idaho, and Montana (Pfister and others 1977; Steele and others 1981, 1983).

However, whitebark pine is relatively intolerant to shade and highly sensitive to competition (Arno and Weaver 1990). Therefore it is frequently restricted to tougher sites that prevent or restrict the growth of other

Table 5—Number and infection of whitebark pine seedlings in four clearcuts

Name of clearcut	Seedlings per hectare	Blister rust infection
		Percent
Vermillion Pass	445	55
Upper Coal Creek	1,544	4
Upper Big Creek	884	33
Divide Mountain	3,929	52

Table 6—Variation in various traits of whitebark pine for 10 provenances

Provenance	Lat.	Long.	Preliminary population comparisons				
			Elevation	Third-year height	Red stem	Ext bud	Blister rust
			<i>m</i>	<i>cm</i>	----- Percent -----		
Cooper Pass	47-32N	115-44W	1,494	17.1	22	9	22
Gisborne	48-21N	116-44W	1,692	15.0	10	4	24
Freezeout	47-01N	116-02W	1,707	10.6	3	0	5
Lunch Peak	48-22N	116-22W	1,982	16.9	10	9	33
Brundage Mountain	45-01N	116-07W	2,195	16.2	17	8	24
Seven Devils	45-21N	116-31W	2,302	12.8	6	3	26
Saddle Mountain	45-42N	113-59W	2,378	18.1	24	2	46
Porphyry Peak	46-49N	110-44W	2,509	12.0	0	13	33
Boulder Peak	41-35N	123-05W	2,523	10.7	0	0	—
Palmer Mountain	45-04N	110-35W	2,652	16.3	0	22	41
Mean				14.6	9	7	25

species. Because of the combination of several severe environmental factors, such as short growing season, cold air, and snow blast (McCaughey and Schmidt 1990), whitebark pine forms krummholz stands of shrublike trees at or near timberline. At lower elevations, where growing conditions are not quite so severe, whitebark pine grows in nearly pure stands of trees 30 to 90 feet tall (McCaughey and Schmidt 1990). When environmental conditions are even less severe, whitebark pine is associated with other tree species and takes on a form much like lodgepole pine. When growing conditions are ideal, whitebark pine seedlings will grow fairly rapidly (fig. 4).

With such a wide-ranging and ecologically diverse species one would expect several geographic races. Since nutcrackers normally cache the seed at least several hundred meters and in many cases several kilometers from its source, it is also easy to speculate that there are few races because genes from several diverse populations are being continually mixed. Future tests should clarify this puzzle.

Seed from about 40 stands have been collected. Our first area of study will be Idaho and Montana. The test will be established with seed from about 100 populations. A preliminary test has revealed some interesting data (table 6). There is considerable variation among the populations in 3-year-old total height (fig. 4). The tallest seedlings were from the Saddle Mountain stand—a population from high elevation. There is also high variation among families within stands (table 7). Also, characteristics such as red coloration of the succulent stem and the proliferation of lateral buds vary with population (fig. 5). So far, none of this variation can be associated with geographic position or elevation.

Inbreeding—In many stands, only a few individuals remain. This results in much higher opportunity for self-fertilization (inbreeding). At what level will inbreeding adversely affect growth and survival of the seedlings? A study has been initiated to compare growth and other traits between a highly decimated population and a stand with very low mortality. Trees at the two sites will be intercrossed, crossed with pollen from the same site, and compared with wind-pollinated seed.

BREEDING PLANS TO DEVELOP RESISTANCE

Our surveys have shown that there are many phenotypically resistant whitebark pine trees. A traditional breeding approach could be used to develop a new blister rust-resistant variety of whitebark pine from these trees. Three options in this approach will be discussed. However, because of the high level of natural regeneration of whitebark pine in clearcuts and burns adjacent to high-mortality stands, another approach appears more attractive. This is a more natural method using mass selection as the genetic selection system, but within a natural setting and with natural selection processes.

The Traditional Approach (fig. 6)—Steps to success are:

1. Locate blister rust-resistant phenotypes of whitebark pine. Most stands have a few candidate trees, but a high number is required so that we can be assured of



Figure 4—Three-year-old container-grown whitebark pine.

Table 7—Variation among whitebark pine families within the Gisborne Stand

Family	Third-year height	Red stem	Prolific bud	Blister rust
	cm	----- Percent -----		
1	18	6	0	11
2	12	11	0	22
3	16	0	0	29
4	14	12	0	0
5	15	20	5	22
6	14	7	0	14
7	17	0	0	7
8	15	4	13	33
9	18	20	4	65
10	15	9	0	35
11	12	5	9	30
Mean	15	9	3	24

finding several genes for resistance. Thus, many stands will have to be visited. The breeding population for western white pine is over 3,000 phenotypically resistant trees and is considered a minimum number of parent trees to assure maintenance of resistance against several races of the rust fungus.

2. Collect wind-pollinated seed from each tree. In special cases, where there are just one or two trees, artificial pollination by other candidate trees may be advisable.

3. Sow seed, grow seedlings, and inoculate with blister rust in the fall of their second growth period.

4. Data over the next 4 years, after inoculation, will reveal the most resistant parents of the phenotypically resistant candidate trees, along with their resistant progeny.

Options for developing the new resistant variety are:

1. Selected resistant parents can be grafted into a seed orchard.

2. Resistant seedlings can be used to establish a seed orchard.

3. Surviving seedlings from rust tests that were not used in the seed orchard can be outplanted in a natural site. The numbers for this planting can probably be increased by rooted cuttings of the surviving seedlings.

Timing: The first five steps could be done in about 10 years. Time to flowering of grafts could be 10 years, but it will probably take from 40 to 50 years for their progeny to flower. New technology may shorten this time.

Problems:

1. What is the natural level of resistance?

2. How far can seed be transferred without serious maladaptation?

Natural Selection Stand—In many localities in Idaho and Montana whitebark pine has been decimated by blister rust, leaving just a few individuals per hectare. Many of these remnant stands are adjacent to burns or clearcuts. In at least several dozen cases these openings

contain high numbers of whitebark pine seedlings and saplings (table 5). With careful management we may be able to use these newly established stands for our purpose. Only three major steps need to be taken:

1. Select the areas within the clearcuts and burns that will be managed for whitebark pine (fig. 7A).

2. Clean the selected area of competing trees and shrubs (fig. 7B). Whitebark pine is a poor competitor. In fact it probably can be grown at much lower elevations if the site is kept free of competition.

3. Let nature take its course concerning the selection of the most resistant trees (figs. 7C, D).

Problems:

1. What is the natural level of resistance? We need to know the level of resistance (1, 5, or 10 percent) in stands to choose sites that have a good chance for success. If only 1 percent of the seedlings are resistant when produced by a mature stand that has had 90 to 95 percent mortality by blister rust, a candidate area would have to have an unusually high number of seedlings to end up with a reasonably stocked stand. If 10 to 20 percent are resistant, the probability of producing a new stand would be considerably better.



Figure 5—Proliferated lateral buds on whitebark pine.

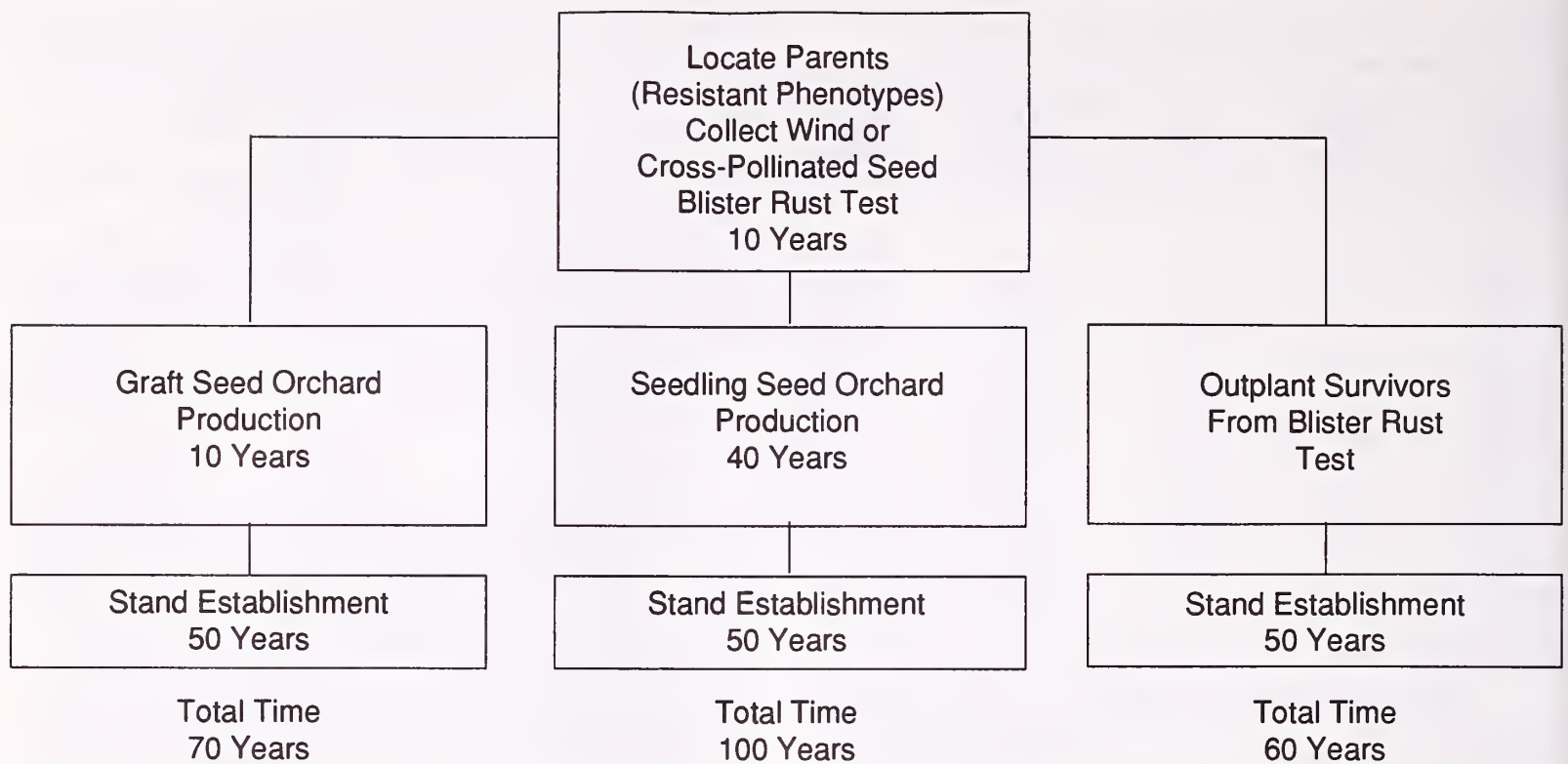


Figure 6—Options for traditional breeding methods for developing new varieties of blister rust-resistant whitebark pine, including completion times.

2. How much inbreeding is occurring in the decimated stands? Severe inbreeding might result in reduced growth and survivability.

3. What is the minimum number of cones and seed needed before seed caches are effective for regeneration? Some sites may be beyond help.

4. When these sites start producing resistant seed how far can the seed be transferred?

Timing (fig. 8): First-generation blister rust selection has already been made on parent trees. Seedling establishment has already occurred on dozens of sites. Natural selection by blister rust is occurring. In 40 to 50 years established stands on preferred sites could be producing cones.

However, it is not only the increase of resistance genes that is important—although this is a key to the species' future—it is important to maintain as much of the natural function of whitebark pine forests as possible. In addition to the severe genetic impact to whitebark pine itself, the critical ecological functions of this species have been threatened by loss of integrity of whitebark pine forests. Thresholds are a key consideration when attempting to restore severely altered ecological systems (Friedel 1991; Laycock 1991). The ecological thresholds for whitebark pine forests are not well understood and with the loss of most of the original structure of these forests much of the integrity has been lost. It will take generations to reproduce nearly pure, mature whitebark pine forests. In the interim, components of the ecological systems most affected by the loss of whitebark pine forests may be irreversibly altered.

Time is of the essence, but all is not lost. Over large areas the first generation is mostly gone, but in many areas

the second generation is there; we must act now to save it. In other areas the first generation is largely intact. In these areas immediate emphasis needs to be placed on retaining or restoring the ecological function of whitebark pine. Protective measures, such as pruning and *Ribes* population manipulation may be used.

What we are trying to say in this section is that there is much that can and must be done immediately to maintain and restore whitebark pine in the ecosystem.

BLISTER RUST ON WHITEBARK PINE, A GENETICS PERSPECTIVE

The general level of resistance of the original population (before the introduction of blister rust) is less than 1 percent. Therefore, the genetic consequence of the blister rust epidemic for most of the range of whitebark pine is to push it through an extremely small bottleneck. In some areas where the number of surviving trees has been reduced to only a few over several hundred hectares, the bottleneck may result in entire populations being lost. Figure 1 indicates geographic populations of whitebark pine that will have the most immediate difficulty (high incidence area), those that will have only minor problems (moderate incidence area), and those that are not likely to have a problem (little or no incidence). Further research clarifying levels of natural resistance will be a significant aid to predicting the adequacy of natural selection in the various areas. On some sites, time alone may return whitebark pine to its former levels; on other sites, whitebark pine may be lost if not aided by genetic improvement and silvicultural programs.

In areas where there are many surviving trees within a very reduced population, the concern will be the damage

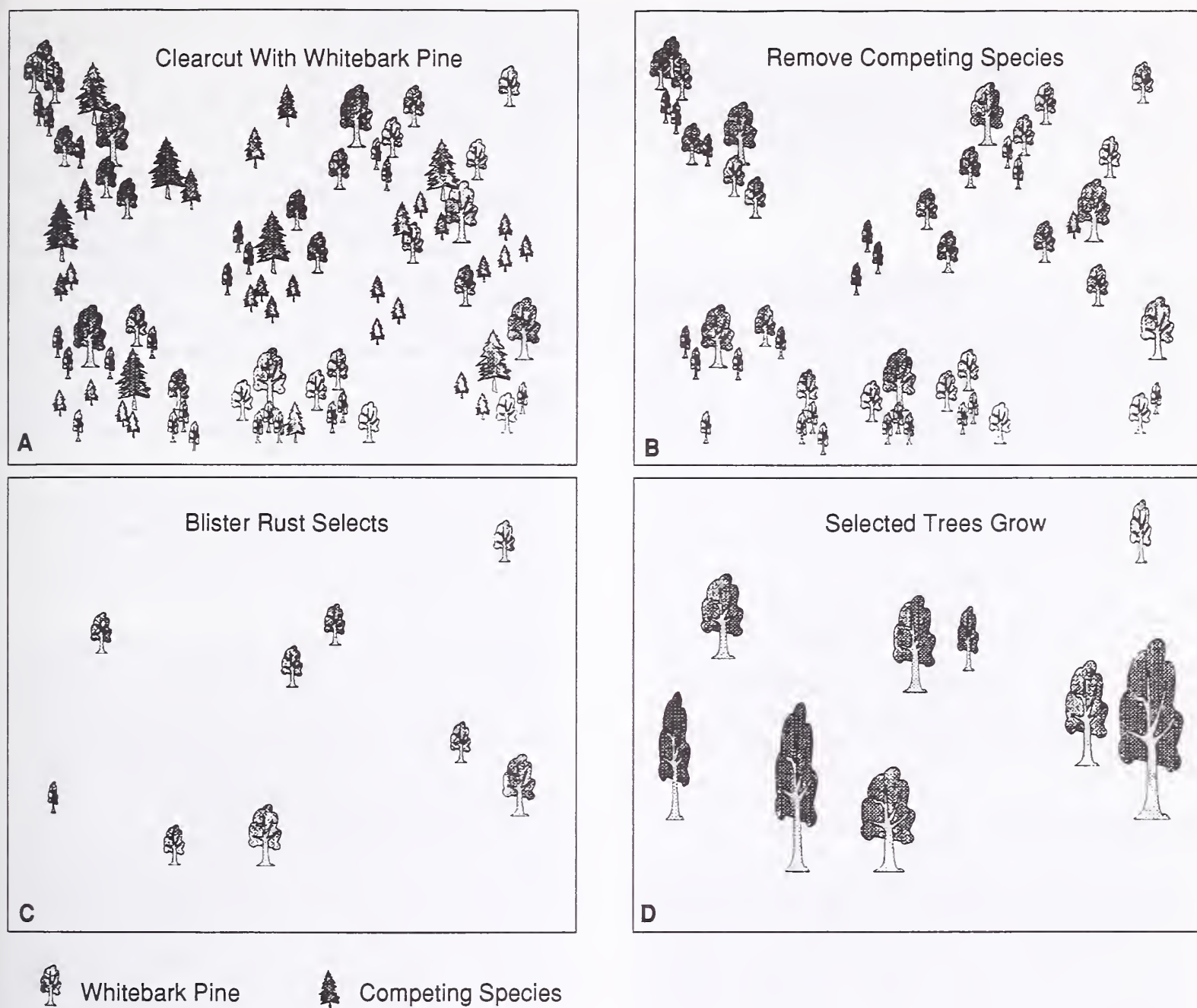


Figure 7—Development of a natural selection stand: A, A clearcut before cleaning containing whitebark pine and competing trees; B, clearcut after cleaning; C, clearcut after infection by blister rust and selection of most resistant trees; D, the natural selection stand or seed orchard after growth of selected trees.

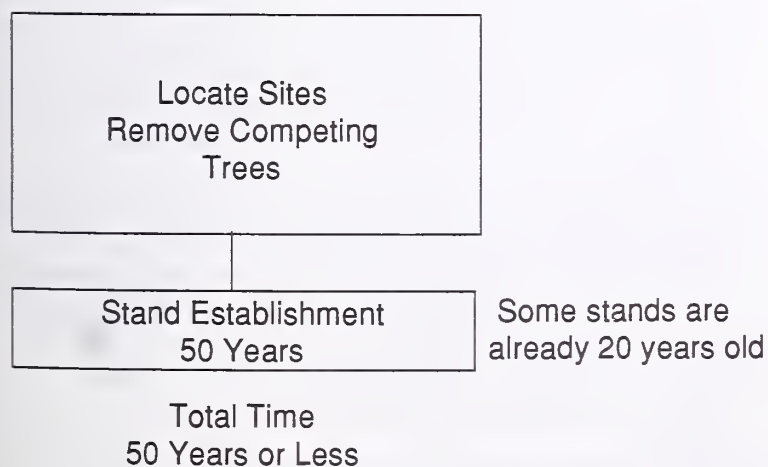


Figure 8—Natural selection method for developing a new variety of blister rust-resistant whitebark pine, including completion times.

done by inbreeding. In most conifers inbreeding is detrimental. Inbred trees generally grow slowly, and detrimental genes such as for albinism, short leaves, and stunted seedlings may often occur. However, whitebark pine is often transported by birds to areas where there is no other whitebark pine (Linhart and Tomback 1985). Because there are only a few individuals in the start-up stand, inbreeding would be high. This may have been the most common way of past population expansion and, over time, lethal and other detrimental genes may have dropped out of the population leaving a species that is not adversely affected by inbreeding.

Even with all these dire genetic consequences, the genetic opportunity for the survival of whitebark pine in the high-mortality zone appears very high, especially with the intelligent help of humans. There are many phenotypically resistant trees. These surely can be used as a base

for new varieties of whitebark pine resistant to blister rust. But most exciting, the high natural regeneration of whitebark pine stands in clearcuts and burns—even in areas where there appear to be insufficient numbers of parent trees—indicates that natural processes are already producing a new variety. Further, these trees are growing well; there do not appear to be inbreeding problems.

CONCLUSIONS

The consequences of the blister rust epidemic have to be viewed as a disaster for whitebark pine, and a setback for Clark's nutcrackers, grizzly bears, and other components of whitebark pine forest ecosystems. Nevertheless, whitebark pine appears to be equipped with elements that will permit survival. Most important is seed caching by the nutcracker even when there is just a small excess. Also, phenotypically resistant trees seem to be fairly common. Considering the low numbers of noncankered western white pine trees together with the much higher susceptibility of whitebark pine, we wonder that there are any whitebark pine trees at all.

Over large areas, the first generation of whitebark pine is nearly gone; however, the second generation is often present. In other areas the first generation is still largely intact. To save whitebark pine and its ecosystem in the most sensitive areas it is essential that we act now. Maintaining sufficient ecosystem function for whitebark pine while developing greater resistance will be a challenge for land managers.

REFERENCES

- Arno, S. F.; Weaver, T. 1990. Whitebark pine community types and their patterns on the landscape. In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 97-105.
- Bedwell, J. L.; Childs, T. W. 1943. Susceptibility of whitebark pine to blister rust in the Pacific Northwest. *Journal of Forestry*. 41: 904-912.
- Bingham, R. T. 1972a. Artificial inoculation of large number of *Pinus monticola* seedlings with *Cronartium ribicola*. In: Bingham, R. T.; Hoff, R. J.; McDonald, G. I., eds. Biology of rust resistance in forest trees. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture: 357-372.
- Bingham, R. T. 1972b. Taxonomy, crossability, and relative blister rust resistance of 5-needled white pines. In: Bingham, R. T.; Hoff, R. J.; McDonald, G. I., eds. Biology of rust resistance in forest trees. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture: 271-280.
- Bingham, R. T. 1983. Blister rust resistant western white pine for the Inland Empire: the story of the first 25 years of the research and development program. Gen. Tech. Rep. INT-146. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 45 p.
- Childs, T. W.; Bedwell, J. L. 1948. Susceptibility of some white pine species to *Cronartium ribicola* in the Pacific Northwest. *Journal of Forestry*. 46: 595-599.
- Childs, T. W.; Bedwell, J. L.; Englerth, R. H. 1938. Blister rust infection of *Pinus albicaulis* in the Northwest. *Plant Disease Reporter*. 22: 139-140.
- Delatour, C.; Birot, Y. 1982. The international IUFRO experiment on resistance of white pines to blister rust (*Cronartium ribicola*): the French trial. In: Heybroek, H. M.; Stephan, B. R.; Weissenberg, K., eds. Resistance to diseases and pests in forest trees. Wageningen: Pudoc: 412-414.
- Friedel, M. H. 1991. Range condition and the concept of thresholds: a viewpoint. *Journal of Range Management*. 44: 422-426.
- Hoff, R. J.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. *European Journal of Forest Pathology*. 10: 307-316.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management*. 44: 427-433.
- Linhart, Y. B.; Tomback, D. F. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. *Oecologia*. 67: 107-110.
- McCaughey, W. W.; Schmidt, W. C. 1990. Autecology of whitebark pine (*Pinus albicaulis* Engelm.). In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 85-96.
- McDonald, G. I.; Hoff, R. J. 1970. Resistance to *Cronartium ribicola* in *Pinus monticola*: early shedding of infected needles. Res. Note INT-124. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p.
- Pfister, R. D.; Kovalchick, R. L.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.
- Spaulding, P. 1911. The blister rust of white pine. Bull. 206. Washington, DC: U.S. Department of Agriculture, Bureau of Plant Industry. 88 p.
- Steele, R.; Cooper, S. V.; Ondov, D. M.; Roberts, D. W.; Pfister, R. D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.
- Steele, R.; Pfister, R. D.; Ryker, R. A.; Kittams, J. A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.
- Stephan, B. R. 1985. Resistance of five-needle pines to blister rust. *Allgemeine Forstzeitschrift*. No. 28: 695-697.
- Yokota, S. 1983. Resistance of improved *Pinus monticola* and some other white pines to the blister rust fungus, *Cronartium ribicola*, of Hokkaido, Japan. *European Journal of Forest Pathology*. 13: 389-402.

PERFORMANCE OF *PINUS CEMBRA*, *P. PEUCE*, AND *P. STROBIFORMIS* WITHIN AIR-POLLUTED AREAS

Karel Kaňák

Abstract—An inventory of the surviving species within the heavily air-polluted area of the Ore Mountains showed a number of species of the genus *Pinus* without symptoms of injury. Three species of the stone pines are described to demonstrate the importance of the geological past of the species. It relates to the impact of the catastrophes and volcanic activities and sudden changes of climate for the species' preadaptation to the toxic impact of a changing environment. The causes of the resistance seemed to be connected with the long-term migration (*Pinus cembra*, *P. peuce*) and hybrid origin (*P. peuce*, *P. strobiformis*). The importance of the life history of the species is unquestioned.

During the years 1956 until 1966 the author (Kaňák 1971, 1988, 1991) established an international collection of species of genus *Pinus* in Plzeň, West Czechoslovakia, in the forest locality of Sofronka (latitude 50° N.).

Various species of pines are represented in Sofronka either by patterns of populations that come from different localities within every species range or from groves of individual trees from species that originated from locations that were not sufficiently preadapted for the local conditions of the new environment (Kaňák 1988). A research center was established at the Arboretum Sofronka in 1963 to investigate evolution of the species included within the collection. The entire range of provenance experiments with some of the species was analyzed with respect to the evolution of their distribution area during postglacial time.

The air pollution caused by extensive industrial emissions resulted in a mass extinction of the Norway spruce forests in the Ore Mountains in the vicinity of Plzeň. In the first stage of the extinction, the dying spruce stands were cleared, but small groves of individual trees, predominantly the local and exotic species of pines, survived. Therefore, the staff of the research center at Sofronka was invited to join the search for an ecologically harmless method of reconstructing the extinct forests.

Some species of white pines were discovered whose needles appeared to be unaffected by emissions. These species of stone pines were: Swiss stone pine (*Pinus cembra* L.), Macedonian pine (*Pinus peuce* Griseb.), and southwestern white pine (*Pinus strobiformis* Engelm.). Their unique viability had helped them to survive under the highly unfavorable conditions.

SWISS STONE PINE

1. Occurs as individual trees in the entire emission area between the town of Hora Sv. Sebestiána and Mount Klínovec (1,210 m above sea level [a.s.l.]). Some trees, otherwise injured by snow and icing, show no injury from emissions. Many of them bear germinant seeds (Mottl and Prudic 1982).

2. One grove of fertile trees 60 to 70 years of age occurs in the cemetery arboretum in the town of Vejprty. Their dimensions are 12 cm diameter at 1.3 m and 9-11 m height. They bear germinant seeds.

MACEDONIAN PINE

On the Saxon side of the mountains:

1. Forest district Steinbach, Department 157a2, elevation 800 m a.s.l. A group of 17 trees, age of 55 years, fertile, with natural regeneration. Dimensions: Diameter 26-35 cm at 1.3 m and 15 m height.

2. Forest district Schmalzgrube, Department 291a3, elevation 900 m a.s.l. Twelve trees of the same provenance and age as the latter growing on a peat bog! The trees are healthy and fertile. Dimensions: Diameter 15-40 cm at 1.3 m and 11-14 m height. Tree trunks have been injured by the red deer and humans (climbing spurs).

3. Forest district Grumbach, Department 331a4, elevation 825 m a.s.l. Stand area is 0.75 ha and trees are 50 years old (1982) and grow in a mixture with *Pinus contorta* ssp. *latifolia* and the mountain variant of *Pinus sylvestris* L. Average height of the stand is 18 m, diameter is 21-35 cm at 1.3 m. Macedonian pine is the most vital of the named species.

On the Czech side of the mountains:

1. Locality Bludna, Forest Management Horní Blatná, elevation 1,000 m a.s.l. Northern slope stand of approximately 200 trees, age probably 70 years. Origin unknown, but probably from activities of the Forest Research Institute Mariabrunn just before World War I. Many trees were apparently broken at the height of 5-7 m, but replacement crowns are now reaching heights of 15 m. Trees are relatively fertile with natural regeneration present.

SOUTHWESTERN WHITE PINE

1. Locality: Cemetery arboretum in the town of Vejprty with a heavy emission impact. One tree only. Diameter 36 cm at 1.3 m, height 14 m, and age 50-60 years. Tree is fertile with germinant seeds in the cones lying on the moist grass!

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Karel Kaňák, National Park of Sumava, Vimperk, Czechoslovakia.

PROBABLE CAUSES OF RESISTANCE

Autochthonous Species

Ten years of observations and experimental activities in the 7-year period 1982-89 give us the following indications:

Variability—Among the local forest tree species, there are different degrees of resistance between individual trees within the stands. Both autochthonous and allochthonous pine species had been gradually reduced, but there are some examples without any symptoms of injury. Fir disappeared on the Czech side of the mountain range first, but drought rather than emissions may have been the cause. Norway spruce seems to be extinct.

Catastrophic Selection—Norway spruce mostly disappeared in a relatively short time—about 6 years. However, after its massive extinction, individually resistant trees of this species were found within the extinct forests. This appearance is commonly known under the term “population bottleneck” (Dobzhanski and others 1976) or “catastrophic selection” (Lewis 1962; Raven 1964) or “une évolution accélérée” (Bouvarel 1960).

Founder Effect—According to Mayr’s “founder-effect” (Mayr 1942, 1965, 1979) after the strong reduction of Norway spruce the reconstruction of its genetic architecture within the small number of survivors (founder population) might follow (Kaňák 1988). This might give rise to a new species population endemic to the environmental conditions that caused the latter extinction.

Allochthonous Species

Hybridization—The Canadian species of spruce show a high degree of emission resistance compared to the local Norway spruce. Their life history, with their intricate genetic relations, may help explain this orientation (Heimburger and others 1983; Morgenstern and Farrar 1964). Morphological and genetic evidence indicates that black spruce is a relatively young species. It is thought to be of an American origin resulting from the hybridization of a proto-white spruce from eastern Asia migrating eastward with a proto-red spruce of North American origin migrating westward. Differences in morphological characteristics between black spruce and red spruce in the direction of white spruce would indicate such hybrid origin (Heimburger 1983).

Directional Selection

The most relevant information came from all the foreign species formerly introduced to this mountain range. An excellent example is the life history of lodgepole pine as described by Hansen (1942, 1943). This species came from the Cascade Range territories of North America where it had been influenced by repeated volcanic activity. Consequently, many generations of lodgepole pine were subjected to directional selection through the toxic air and soil, and lodgepole pine adapted to become the founding pioneer stage of the ecosystems’ evolution.

Migration Preadaptation

The other very important evolutionary factor is migration. It acts on the development of ecological potentials as a consequence of the tolerance to the extreme environmental conditions (toxic sites), the environmental changes, and all the preadaptations that could be acquired only during a long migration route such as those in the Tertiary—one from eastern Asia to southern Europe (Mirov 1967) and the other from eastern Asia to Australia (Mayr 1965).

HISTORY OF SPECIES

Mirov (1967) located the center where the genus *Pinus* originated in Eastern Asia, where catastrophes like volcanic activity and changes in climate gave all the species of pines a specific starting point to their principal adaptation.

“Pines however possessed two characteristics since the Mesozoic origin of the genus: their xeromorphy and their ability to endure direct sunlight. These characteristics may be considered as generally the same throughout the whole paleobotanical history.” (Mirov 1967).

Pinus cembra

“During the Ice Age, the high mountain pines of the Alps either perished or were preserved in the lower areas not covered with ice. *Pinus cembra* found occasionally in northern Italy is the relic preserved in one of such refugia (Emberger 1944). With subsequent warming up, it migrated again to the high elevations of the central Alps. There is, of course, a possibility of the existence of non-glaciated refugia even in the central parts of the Alps. *Pinus cembra* might have survived in some of these few areas that remained free from the ice.” (Mirov 1967).

The indications are that *P. cembra* and many other species of the eastern Asia flora migrated to the Alps during the Tertiary. During the last glaciation they occurred in an almost continuous belt of higher elevations. Consequently, because of the enlarged area of its distribution, *P. cembra* developed a well-supported degree of genetic variability. This species of stone pine survived the last glaciation, and within its refugia there was probably an increasing frequency of autogamy that must be taken into account (Bannister 1965). After the retreat of the glacier, the migrating progenies probably intercrossed at their contact zone and thus acquired their increasing variability as well. Together with the very short period of the last glaciation, the undiminished variability still maintains itself today. *Pinus peuce* apparently has a similar pattern of the life history.

Pinus peuce

According to Mirov, “There are indications that Mediterranean pines migrated from eastern Asia along the mountain ranges, that once extended north of and parallel to Himalaya.” (Mirov 1967).

“Endemic *Pinus peuce* is very local in Bulgaria, Albania and Yugoslavia. It is a haploxyton pine closely related to

Pinus griffithii of the Himalaya. Before the great migration, *Pinus peuce* has been crossed with other haploxyton pines. Judging by the chemical composition of its turpentine (Illoff and Mirov 1956) it has a close affinity to eastern Asiatic and western American pines" (Mirov 1967).

The hybridization should be a source of variation for adaptation to new environments (Lewontin and Birch 1966).

The whole Mediterranean region experienced many tectonic changes throughout the Tertiary. In the Quarternary there occurred intensive faulting and sinking of considerable areas. This resulted in the formation of separate mountain ranges and many islands. As a consequence, the present distribution of pines in the Mediterranean region is sporadic and irregular (Mirov 1967).

Pinus strobiformis

Southwestern white pine appear to have morphological indications of a hybrid origin. Critchfield and Little (1966) said: "This species forms a link both geographically and morphologically, between the neighbors *Pinus flexilis* and *Pinus ayacahuite*. Southwestern pine is apparently separated from its southern relative *Pinus ayacahuite* by a 100 mile gap that does not seem to correspond to any comparable discontinuity in suitable habitats."

We have population samples of *Pinus strobiformis* in our arboretum that originated from Greenlee, AZ, at latitude 33°39' N., longitude 109°16' W., elevation 2,740 m a.s.l. This stand is now 30 years of age. Its fertility began at the age of 22 years. Its cones are surprisingly variable in size, from the smaller cones similar to *Pinus flexilis* to very big cones with apophyses, similar to *Pinus ayacahuite* var. *brachyptera*. Such a variation supports the hypothesis about the hybrid origin of this species.

TESTS OF SPECIES POTENTIALS

The response of a species to the impact of an environmental stress allows us to recognize intrinsic characteristics and appearances that we do not usually encounter under normal circumstances. Therefore, we are focused on testing the collection of pine species at the arboretum within the zone where there is a heavy impact of both emissions and severe mountain climates.

CONCLUSIONS

The threatened trees of some forest species under heavy emissions often show a surprising ability to endure the selection pressure of the toxic environment. Evidently this depends on the life history of the species in question. Some conditions under which we feel the tested species have a better predisposition to survive are:

1. The species is of hybrid origin.
2. The species has undergone a long-term intercontinental migration.
3. The species has been subjected to repeated strong directional or even catastrophic selection under the impact of volcanic activity. Volcanic areas are noted for their toxic air and soil similar in some ways to industrial emission areas.

REFERENCES

- Bannister, M. H. 1965. Variation in the breeding system of *Pinus radiata*. In: Baker, H. G.; Stebbins, G. L., eds. The genetics of colonizing species. In: Proc. First Int. Un. Biol. Sci. Symp. Gen. Biol. Davis; 1964 February. New York and London: Academic Press: 353-374.
- Bigelow, R. S. 1965. Hybrid zones and reproductive isolation. *Evolution*. 19: 449-508.
- Bouvarel, P. 1960. Note sur la résistance au froid de quelques provenances de pin maritime. *Revue forestière française*. 7: 495-508.
- Critchfield, W. B.; Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Diels. 1910. ex Mirov (1967).
- Dobzhanski, Th.; Ayala, F.; Stebbins, L. G.; Valentine, L. W. 1976. *Evolution*. San Francisco: Freeman.
- Emberger. 1944. ex Mirov (1967).
- Hansen, H. 1942. The influence of volcanic eruptions upon post-Pleistocene forest succession in central Oregon. *American Journal of Botany*. 29: 214-219.
- Hansen, H. 1943. Paleocology of the sand dune bogs on the southern Oregon coast. *American Journal of Botany*. 30: 335-340.
- Heimbürger, C. C. 1983. The evolution of Black spruce. Proc. XIX. Meet. CTIA, Part 2: 163-166. Toronto.
- Illoff, P. M., Jr.; Mirov, N. T. 1956. Composition of gum turpentines of pines. XXV. A report on two white pines: *Pinus koraiensis* from Korea and *Pinus peuce* from Macedonia. *Amer. Pharm. Ass. J. Sci. Ed.* 45: 77-81.
- Kaňák, K. 1971. Arboretum Sofronka. Introduction results in 1958-1968. Praha. 38 p. illus.
- Kaňák, K. 1988. Contribution to maintaining continuity of the Norway spruce in the Ore Mountains. *Folia Mus. Rer. Natur. Bohem. Occid. Plzeň, Botanika* 27. 58 p.
- Kaňák, K. 1991. Colonizing ability of some introduced species of pines. *Folia dendrologica*. 18: 187-200. Veda, Bratislava.
- Lewis, H. 1962. Catastrophic selection as a factor in speciation. *Evolution*. 16: 257-271.
- Lewontin, R. C.; Birch, L. C. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution*. 20: 315-336.
- Mayr, E. 1942. *Systematics and the origin of species*. New York: Columbia University Press.
- Mayr, E. 1965. Summary. In: Baker, H. G.; Stebbins, G. L., eds. The genetics of colonizing species. In: Proc. First Int. Un. Biol. Sci. Symp. Gen. Biol. Davis; 1964 February. New York and London: Academic Press: 553-562.
- Mayr, E. 1979. *Evolution und Vielfalt des Lebens*. Springer-Verlag.
- Mirov, N. T. 1967. *The Genus Pinus*. New York: Ronald Press.
- Morgenstern, E. K.; Farrar, J. L. 1964. Introgressive hybridization in red spruce and black spruce. Tech. Rep. 4. Faculty of Forestry, Univ. of Toronto.
- Mottl, J., Prudič, Z. 1982. Analýza růstu limby na Klínovci—v Krušných horách a její roubavanci. *Tschechisch. Zprávy les. výzkumu* 27(4): 9-13.
- Parsons, P. A. 1963. Migration as a factor in natural selection. *Genetica*. 33: 184-206.
- Raven, P. 1964. Catastrophic selection and edaphic endism. *Evolution*. 17: 336-338.

COMPETITION AND CROWN CHARACTERISTICS OF WHITEBARK PINE FOLLOWING LOGGING IN MONTANA, U.S.A.

Todd Kipfer
Katherine Hansen
Ward McCaughey

Abstract—This study was designed to evaluate crown development of whitebark pine (*Pinus albicaulis*) subjected to intertree competition in young mountainous stands in the Yellowstone area. A distance-dependent competition index was used to assess intertree competitive effects on crown growth. Significant inverse correlations were found between the competition index and height, crown diameter, crown diameter/height, and crown volume; however, only 20 percent of the variation was explained by measured variables. Competition thresholds, indicating when crown growth becomes limited, were estimated. In future studies, crown vigor or density measures could perhaps yield a better competition indicator.

This study addresses the response of regenerating whitebark pine (*Pinus albicaulis*) to competition following logging. Human activities, such as logging, in the mountainous environments of western North America are creating a variety of impacts at both the individual scale and at the ecosystem scale. Concern about regeneration crown growth and future cone production in logged sites prompted this study. Cone production is a product of mean shoot production multiplied by the number of fertile shoots (Weaver and Forcella 1986). Effects of competition were hypothesized to affect crown development of whitebark pine. Intertree competition was measured on individual, regenerating whitebark pine in logged sites in southwestern Montana near Yellowstone National Park. This study is part of a larger research project conducted by Kipfer (1992).

Whitebark pine are found on sites with a wide range of geologic, geomorphic, and ecologic conditions (Hansen-Bristow and others 1990). Their growth characteristics depend on numerous factors, including competition, that vary spatially and temporally. Quantifying the influence of competing vegetation on conifer growth may help to determine silvicultural prescriptions such as thinning intensity, optimize management decisions, and provide a basis

for growth models of young forest stands (Wagner and Radosevich 1991b). For example, one management option for whitebark pine is to increase or sustain seed production for regeneration and for a food source for the Clark's nutcracker (*Nucifraga columbiana*), the red squirrel (*Tamiasciurus hudsonicus*), the grizzly bear (*Ursus arctos horribilis*), and a host of other birds and mammals (Craighead and others 1982; Kendall 1983; Kendall and Arno 1990; McCaughey and Schmidt 1990). Seed production may increase with wider, more diffuse crowns (Eggers 1986; Spurr and Barnes 1980), and, therefore, silvicultural prescriptions that increase crown diffusivity are desirable. The effects of silvicultural management options for maintaining or enhancing whitebark pine ecosystems have had limited study (Eggers 1990; Schmidt and McCaughey 1990).

PREVIOUS STUDIES

Whitebark pine is considered relatively intolerant of competition and shade (Arno and Weaver 1990), although the trees may be more shade tolerant at an early stage and less tolerant at later developmental stages (McCaughey and Schmidt 1990). Although initial observations by Eggers (1990) indicate that suppressed whitebark pine seedlings and saplings respond little to the removal of forest competition, the effect of competition on postlogging regeneration needs further study. Weaver and others (1990) assessed competition in terms of stand development and hypothesized that although the density of whitebark pine seedlings remained approximately constant across stands of different ages, growth from seedling to sapling size could not be supported in stands older than 100 years. They suggested that clearings needed to be larger than 10 m² for seedlings to grow to sapling size.

The effect of competition on the growth of individual trees has been studied for many economically important trees in plantations or homogeneous stands (Daniels and others 1986; Tomé and Burkhart 1989; Wagner and Radosevich 1991a,b). These studies have primarily used individual tree growth models based on competition indices and have shown an inverse relationship between the amount of competition from neighbors and individual tree growth performance (Daniels 1976; Daniels and others 1986; Lorimer 1983; Tomé and Burkhart 1989). This study focused on crown development of whitebark pine as related to a distance-dependent competition index. Managers could use this index to determine the optimum

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Todd Kipfer is a Doctoral Student, Department of Geography, Arizona State University, Tempe, AZ 85281; Katherine Hansen is an Associate Professor of Geography, Department of Earth Sciences, Montana State University, Bozeman, MT 59717; Ward McCaughey is a Research Forester, USDA Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT 59717.

spacing or number and spatial arrangement of competitors for maximum crown development of whitebark pine.

METHODS

Three logged stands were sampled in the Gallatin National Forest in southwestern Montana near Yellowstone National Park. The stands ranged in elevation from an average of 2,260 m at Moose Creek to 2,475 m and 2,535 m at Teepee Creek 1 and 2, respectively. The three stands had been clearcut between 1968 and 1972. Data collection focused upon intra- and intertree characteristics for whitebark pine and neighboring trees. One hundred whitebark pine individuals (more than 0.5 m tall) were identified within each of the three stands by a systematic-random sampling procedure along transects. Three different-sized circular plots were nested around each individual whitebark pine. Within each circular plot, trees of specific sizes were identified as competitors using the following criteria: within the 3-m-radius plot, all tree seedlings and saplings were identified as competitors; within the 6-m-radius plot all trees with a diameter at breast height (d.b.h.) greater than or equal to 4 cm and less than 10 cm were identified as competitors; and within the 9-m-radius plot all trees with d.b.h. greater than or equal to 10 cm were identified as competitors. This method approximated a fixed angle gauge sweep (such as that used by Tomé and Burkhart 1989) and requires that trees farther away from the individual tree be larger to be considered competitors.

Five attributes were measured for each whitebark pine: (1) age, (2) height, (3) diameter at breast height (d.b.h.), (4) average live crown diameter, and (5) height of the maximum crown diameter above the ground surface. Crown and height variables were measured to the nearest 0.1 m and d.b.h. to the nearest 0.1 cm.

Total sample size was reduced from 300 to 220 after tree ages showed that some selected whitebark pine indicated some had established prior to logging (advance regeneration). It is difficult to evaluate intertree competition prior to logging, and these were therefore eliminated from further study. A ratio of crown diameter to tree height (CD/H) was computed to reflect the degree of horizontal crown growth. Crown volume was computed using the cone volume equation: ($\text{Volume} = 1/3 * \pi * R^2 * H$). Measurements on competing trees within the 9-m-radius plot were tree species, total tree height, diameter at breast height, and distance (measured to nearest 0.1 m) to the subject whitebark pine.

A distance-weighted size-ratio index or distance-diameter index (Alemdag 1978; Daniels 1976; Hamilton 1969; Hegyi 1974; Tomé and Burkhart 1989) was selected to develop a competition index, from which intertree competition could be quantified. The distance-diameter index is a distance-dependent index that sums a size ratio of diameters (d.b.h. or basal diameter) of competing trees to the diameter of a subject tree. The general theory is that larger competing trees, relative to the individual tree, contribute more competition than do smaller trees. The index also assumes that competitive influence decreases with increasing distance between the individual tree and the competitor.

The distance-diameter index was modified for whitebark pine because the trees often had multiple stems or did not reach breast height. Height was substituted for diameter and distance weighting functions were applied to develop the modified competition index:

$$C.I. = \sum_{i=1}^N (H_j/H_i) * \text{function}(DIST_{ij})$$

where C.I. is the competition index; H_j is the tree height of the subject tree; H_i is the tree height of the competing tree; and $DIST_{ij}$ is a distance decay function. Three distance decay functions were used: ($1/DIST_{ij}$, $1/DIST_{ij}^2$, and $e^{-DIST_{ij}}$).

Regression analysis was used to evaluate the relationship between competition and crown characteristics of the whitebark pine. The three distance-decay functions were used as dependent variables and tree height and three crown measures (crown diameter, crown diameter to tree height ratio, and crown volume) as independent variables.

RESULTS

Competition index values varied according to the form of the distance-decay function used for whitebark pine. Index values calculated using $1/\text{distance}$ and $1/\text{distance}^2$ were similar with mean values ranging from 13.12 to 17.12. Index values using the $e^{-\text{distance}}$ decay function ranged from 3.11 to 4.22.

Tree heights of whitebark pine were significantly correlated ($P = 0.007$) with the competition index; however, R^2 values for the three distance-decay functions (0.033 for $1/\text{distance}$, 0.027 for $1/\text{distance}^2$, and 0.032 for $e^{-\text{distance}}$) indicate that the linearity of that relationship is poor as shown for $1/\text{distance}$ in figure 1. The intercept value in the regression equation ($y = a + bx$) was 2.047, which may represent maximum tree heights for whitebark pine in the age classes represented by this study, when growing in the absence of competition.

Crown diameters of whitebark pine were significantly correlated ($P = 0.000$) with the competition index, shown for $1/\text{distance}$ in figure 1, with R^2 values varying depending on the form of the distance-decay function (0.131 for $1/\text{distance}$, 0.096 for $1/\text{distance}^2$, and 0.128 for $e^{-\text{distance}}$). The intercept value (0.820) of the regression equation poorly represents the maximum possible crown diameter, since crown diameter values above 1.0 m were common.

The crown diameter to tree height ratio and crown volume were significantly correlated to competition index as shown for the $1/\text{distance}$ decay function in figure 1. Regression R^2 values for crown diameter to tree height ratio varied depending on the form of the distance-decay function in the competition index equation (0.122 for $1/\text{distance}$, 0.079 for $1/\text{distance}^2$, and 0.120 for $e^{-\text{distance}}$). Similar regression R^2 values were obtained in correlating competition index with crown volume using the three forms of the distance-decay function (0.092 for $1/\text{distance}$, 0.058 for $1/\text{distance}^2$, and 0.091 for $e^{-\text{distance}}$).

The $1/\text{distance}$ decay function in the competition index model yielded slightly higher R^2 values for tree height, crown diameter, crown diameter to tree height ratio, and crown volume of whitebark pine. The $1/\text{distance}$ decay

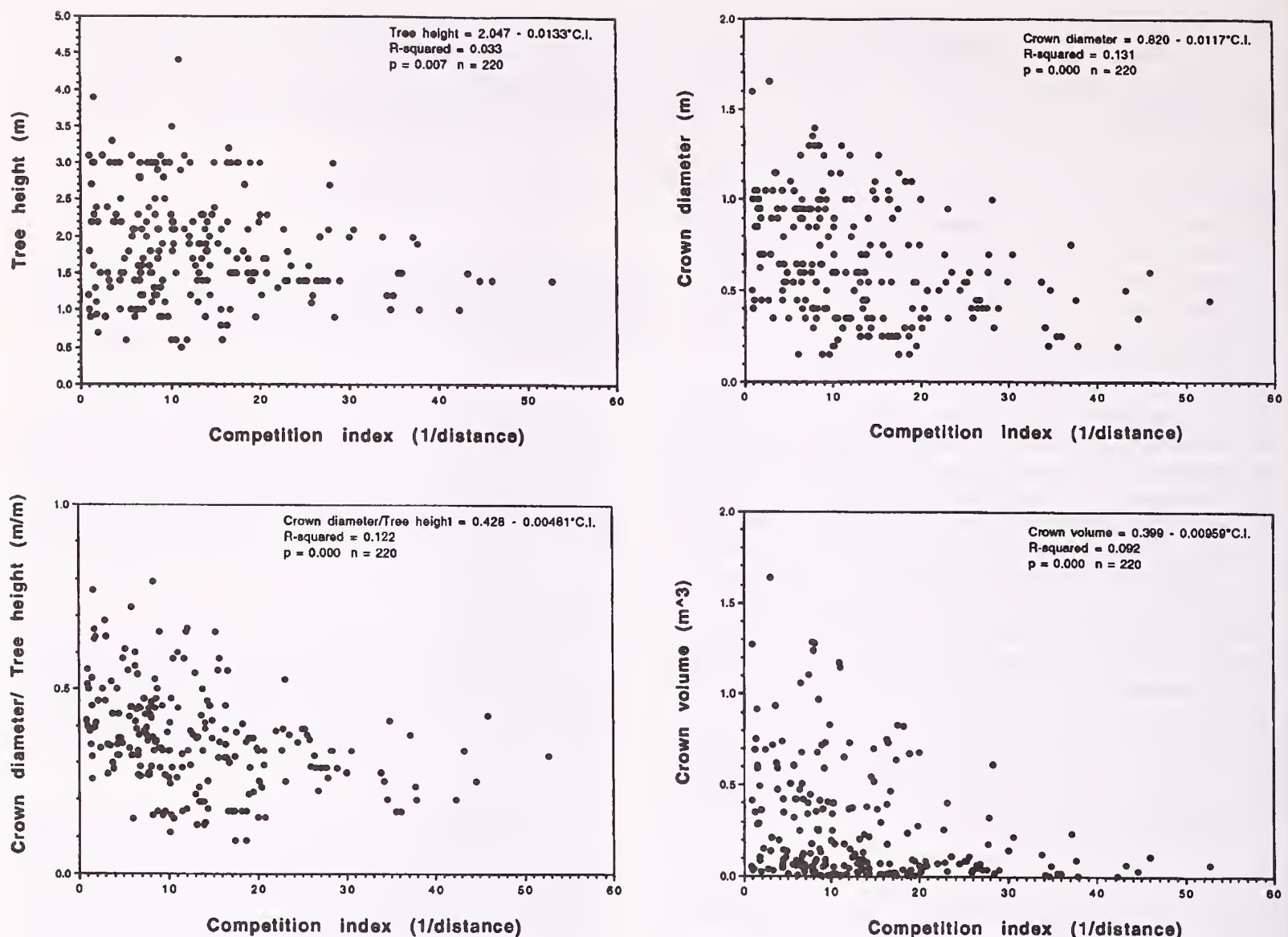


Figure 1—Bivariate scatterplots of total tree height, crown diameter, crown diameter/height, and crown volume of whitebark pine plotted against competition index using a distance-decay function of 1/distance. Regression values shown are model and model coefficients, R -square, p -level, and sample size (n). (Data from all three study sites—Moose Creek, Teepee Creek 1, and Teepee Creek 2.)

function was used for development of a potential competition threshold because it was consistently a stronger predictor of the four growth variables.

Scatterplots were evaluated from each study site for competition index values above which there was visually less variability in the data. No identifiable threshold was observed for whitebark pine in the Moose Creek stand, and therefore, in order to increase the sample size, the two Teepee Creek stands were combined. Potential competition thresholds were estimated for total tree height, crown diameter, crown diameter to tree height ratio, and crown volume for sampled whitebark pine in the two Teepee Creek stands (fig. 2). Variability of data below potential competition thresholds indicates that tree growth factors may not be limiting. The majority of whitebark had competition index values below the estimated threshold values.

Regression analysis of the competition index against the four whitebark pine measures using only those trees greater than the threshold values yielded poor results for

tree height ($R^2 = 0.128$, $p = 0.062$, $n = 27$), crown diameter ($R^2 = 0.146$, $p = 0.106$, $n = 18$), and crown volume ($R^2 = 0.091$, $p = 0.120$, $n = 27$). A statistically significant correlation, however, was found between the competition index and the crown diameter to tree height ratio ($CD/H = 0.846 - 0.0142 \cdot \text{C.I.}$; $R^2 = 0.230$, $p = 0.000$, $n = 18$).

DISCUSSION

The specific competition index values developed by this study explain approximately 20 percent of the variation in competitive pressure exerted on whitebark pine from the numbers, sizes, and spatial patterns of neighboring trees. Assessment of competition on crown development of whitebark pine is difficult when data come from present spatial relationships and past growing conditions are unknown. Competition was a significant factor influencing crown characteristics of whitebark pine in this study. It is important to note that these results only show that competition is a significant factor influencing whitebark

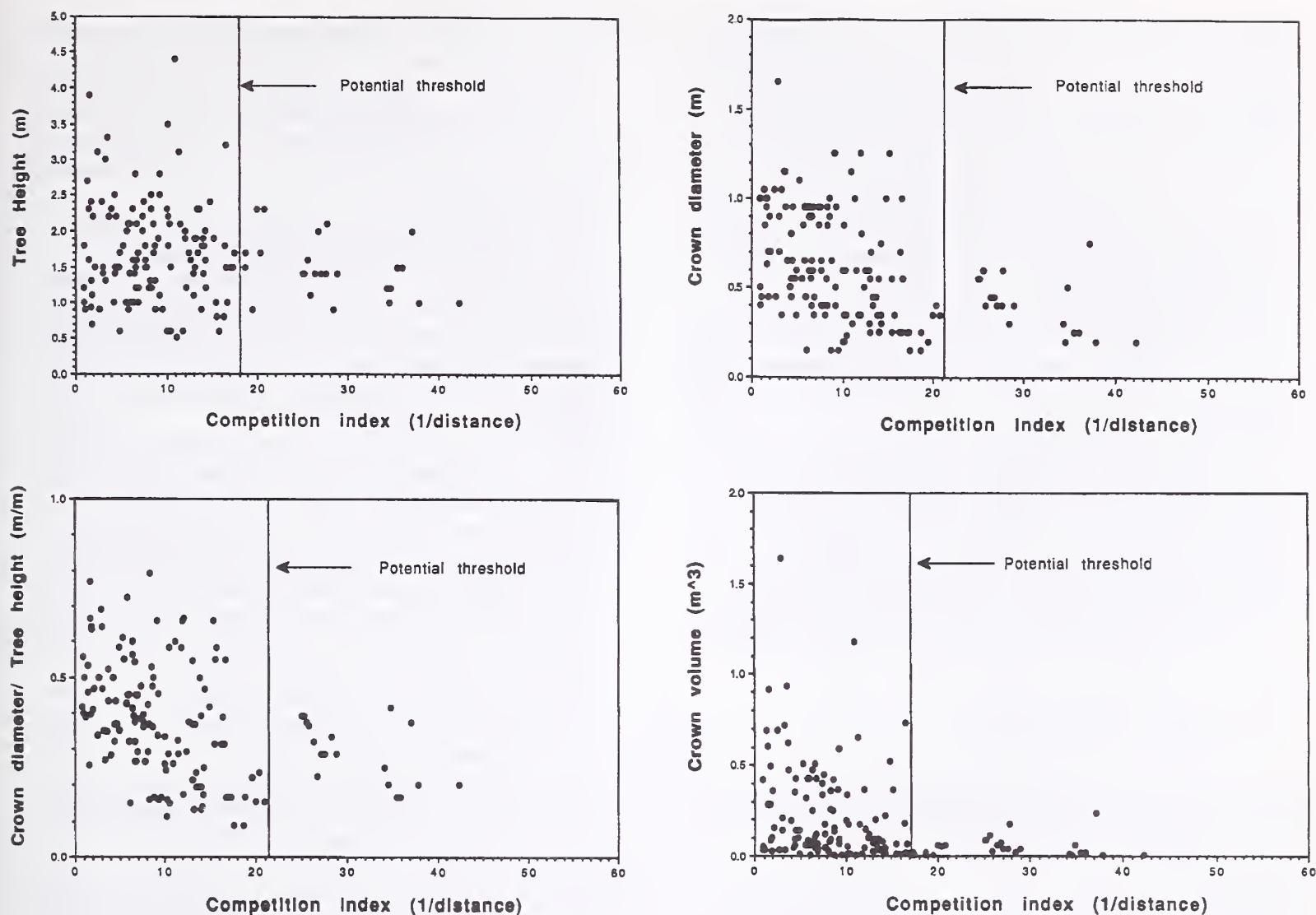


Figure 2—Potential competition thresholds for bivariate scatterplots of total tree height, crown diameter, crown diameter/height, and crown volume of whitebark pine plotted against competition index using a distance-decay function of 1/distance. (Data from Teepee Creek 1 and Teepee Creek 2 only.)

pine. The mechanisms of this competitive influence are unknown.

The distance-decay function $1/\text{distance}$ in the competition index model created an expected inverse relationship of tree growth measure to index. As distance from the subject tree increases effects from competition trees decrease. Tree heights and crown volumes had the poorest correlations with the competition index. Poor correlations with crown volume may be due to sampling procedures. In future studies, crown vigor and crown biomass measurements (stem spacing) might be used to weight crown volume measures, perhaps yielding a better indication of the effect of competition on growth.

Crown diameters and crown diameter to tree height ratios had good correlations with the competition index. Still, only 12 to 13 percent of the variation in these measures was explained by the competition index. The addition of age and an indicator variable for stand improved this relationship for the crown diameter measure, increasing the R^2 value to 0.250. It did not, however, yield a significant correlation for the crown diameter to tree height

ratio. The crown diameter to tree height ratio may represent a characteristic crown shape for young whitebark pine.

Poor correlations between whitebark pine crown characteristics and competition index may be due to factors influencing individual tree size (local density, plant genotype, seed size, emergence time, microhabitat variations, and unknown historical growing conditions). A competition index could incorporate a variety of growing conditions over time and the use of incremental growth characteristics of annual growth could provide some improvement without substantial measurement efforts.

Potential competition thresholds estimated for the two Teepee Creek sites may be artifacts due to relatively few trees with high competition values, or they may be actual values of competitive pressure indicating when growth becomes limited by competition. Multiple-aged stands with varying tree densities should be sampled in future studies. To compare stands of different ages, the age-independent competition index methods of Lorimer (1983) may provide a strong starting point. Although regression analysis can comparatively evaluate the influences of

competitive pressure on whitebark pine characteristics, actual relationships are more complex than the linear regression models might suggest. Nonlinear regression methods should be explored for evaluating competition influences.

Timber harvests provide an important but declining part of our regional economy (Powers 1991), and economic considerations are an important component of forest management policies. Timber harvest can cause accelerated slope failures, erosion, and stream sedimentation from roads (Marston and Anderson 1991) when improperly done. Road building in association with logging provides access to whitebark pine regeneration sites; however, it is not believed that logging will be a major means for regenerating whitebark pine (Arno 1986).

It is imperative to find viable management options for increasing crown growth and the potential for increased cone production for whitebark pine because of its importance to the endangered grizzly and many other wildlife species in the Yellowstone ecosystem. The importance of quantifying how competing trees influence crown characteristics of whitebark pine in logged stands comes from a need to increase our knowledge of how competition affects crown development of whitebark pine.

ACKNOWLEDGMENT

This research was supported in part by funds provided by the Intermountain Research Station, Forest Service, U.S. Department of Agriculture.

REFERENCES

- Alemdag, I. S. 1978. Evaluation of some competition indices for the prediction of diameter increment in planted white spruce. Inf. Rep. FMR-X-108. Canadian Forest Service Forest Management Institute. 39 p.
- Arno, S. F. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-97.
- Arno, S. F.; Weaver, T. 1990. Whitebark pine community types and their patterns on the landscape. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 October 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 97-105.
- Craighead, J. J.; Sumner, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. *Wildlands Inst. Monogr.* 1. Missoula, MT: University of Montana. 279 p.
- Daniels, R. F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. *Forest Science*. 22: 454-456.
- Daniels, R. F.; Burkhardt, H. E.; Clason, T. R. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. *Canadian Journal of Forest Research*. 16: 1230-1237.
- Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. In: Contreras, Glen P.; Evans, Keith E., comps. *Proceedings—grizzly bear habitat symposium*; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.
- Eggers, D. E. 1990. Silvicultural management alternatives for whitebark pine. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 October 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 324-328.
- Hamilton, G. J. 1969. The dependence of volume increment of individual trees on dominance, crown dimensions, and competition. *Forestry*. 42: 133-144.
- Hansen-Bristow, K.; Montagne, C.; Schmid, G. 1990. Geology, geomorphology, and soils within whitebark pine ecosystems. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 October 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 62-71.
- Hegyi, F. 1974. A simulation model for managing jack-pine stands. In: Fries, J., ed. *Growth models for tree and stand simulation*. Res. Notes 30. Stockholm: Royal College of Forestry: 74-90.
- Kendall, K. C. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. In: *Bears—their biology and management*; International Conference on Bear Research and Management. Madison, WI: International Bears Association. 5: 166-173.
- Kendall, K. C.; Arno, S. F. 1990. Whitebark pine—an important but endangered wildlife resource. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 October 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 264-273.
- Kipfer, T. R. 1992. Post-logging stand characteristics and crown development of whitebark pine (*Pinus albicaulis*). Bozeman, MT: Montana State University, Department of Earth Science. 83 p. Thesis.
- Lorimer, C. G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecology and Management*. 6: 343-360.
- Marston, R. A.; Anderson, J. E. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology*. 5(3): 338-346.
- McCaughy, W. W.; Schmidt, W. C. 1990. Autecology of whitebark pine. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 October 29-31;

- Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 85-96.
- Powers, T. M. 1991. Ecosystem preservation and the economy in the Greater Yellowstone Area. *Conservation Biology*. 5(3): 395-404.
- Schmidt, W. C.; McCaughey, W. W. 1990. Whitebark pine—a subalpine species needing silvicultural attention. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 October 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 373-374.
- Spurr, S. H.; Barnes, B. V. 1980. *Forest ecology*. 3d ed. New York: John Wiley and Sons. 687 p.
- Tomé, M.; Burkhardt, H. E. 1989. Distance-dependent competition measures for predicting growth of individual trees. *Forest Science*. 35(3): 816-831.
- Wagner, R. G.; Radosevich, S. R. 1991a. Neighborhood predictors of interspecific competition in young Douglas-fir plantations. *Canadian Journal of Forest Research*. 21: 821-828.
- Wagner, R. G.; Radosevich, S. R. 1991b. Interspecific competition indices and other factors influencing the performance of Douglas-fir saplings in the Oregon Coast Range. *Canadian Journal of Forest Research*. 21: 829-835.
- Weaver, T.; Forcella, F.; Dale, D. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, R. C., comp. Proceedings—conifer tree seed in the inland mountain west symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.
- Weaver, T.; Forcella, F.; Dale, D. 1990. Stand development in whitebark pine woodlands. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 October 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 151-155.

FIRE ECOLOGY OF WHITEBARK PINE FORESTS OF THE NORTHERN ROCKY MOUNTAINS, U.S.A.

Penelope Morgan
Stephen C. Bunting
Robert E. Keane
Stephen F. Arno

Abstract—Fires once occurred at intervals between 30 and 300 years in whitebark pine (*Pinus albicaulis*) forests in the Northern Rocky Mountains, U.S.A., but since the early 1900's fewer fires have occurred, contributing to declining abundance of whitebark pine. In the absence of fire or other major disturbance, whitebark pine is replaced by other conifers on most of the upper subalpine landscape. Whitebark pines often survive low-intensity surface fires. Large stand-replacement fires also benefit this species by creating the open, burned sites where regeneration is most successful.

In the Northern Rocky Mountains of western North America, whitebark pine (*Pinus albicaulis*) historically dominated many upper subalpine forests. These high-elevation forests usually have poorly developed, rocky soils and are often located within wilderness or roadless areas. As a consequence, whitebark pine is seldom harvested for forest products, but it is important for scenic, watershed, and wildlife habitat values.

Whitebark pine dominates middle- and late-successional stages. In the absence of major disturbance, however, whitebark pine is eventually replaced by the more shade-tolerant subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) in most of its range in the upper subalpine forest zone of the Northern Rocky Mountains (fig. 1). Whitebark pine is a common seral component of upper subalpine forests found on the *Abies lasiocarpa*/*Vaccinium scoparium*, *A. lasiocarpa*/*Luzula hitchcockii*, and *A. lasiocarpa*/*Arnica cordifolia* habitat types (Pfister and others 1977; Steele and others 1981, 1983; Weaver and Dale 1974). These sites are cold, with July mean temperatures averaging 13 to 15 °C (Pfister and others 1977). Although annual precipitation averages 610 to 1,780 mm, summer drought is common (Arno and Hoff 1989; Pfister and others 1977; Weaver and Dale 1974).

Whitebark pine is also found in pure stands on relatively dry and severe, windswept sites near timberline where it is the climax tree species (Arno and Hoff 1989). It is the sole climax tree species on *Pinus albicaulis* habitat types in Montana, central Idaho, and western Wyoming, and in southern Canada (Arno and Hoff 1989; Steele and others 1981, 1983). Whitebark pine and subalpine fir are climax codominants on the *Pinus albicaulis*-*Abies lasiocarpa* habitat types where subalpine fir growth is stunted in the severe microclimate (Pfister and others 1977). Climax whitebark pine forests are usually open, with small patches of trees of mixed ages interspersed with meadows (fig. 2). Average July mean temperatures are 10 to 12 °C with severe summer droughts and frosts; the annual precipitation of 71 to 153 cm falls mostly as snow (Arno and Hoff 1989; Pfister and others 1977).

Fires are very important to regeneration and survival of whitebark pine on sites where it is seral. Whitebark pine often survives these low-intensity surface fires, which more easily kill associated conifers (fig. 3). Stand-replacing fires also benefit whitebark pine, for although all trees are usually killed, whitebark pine regenerates on burned sites more successfully than many associated tree species (Tomback



Figure 1—Subalpine fir and Engelmann spruce now dominate many stands and whole landscapes where whitebark pine was historically abundant. Whitebark pine is declining in abundance even where blister rust is uncommon, such as on this site east of Yellowstone National Park in Wyoming.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Penelope Morgan is Associate Professor, Department of Forest Resources, University of Idaho, Moscow, ID 83843; Stephen C. Bunting is Professor, Department of Range Resources, University of Idaho, Moscow, ID 83843; Robert E. Keane and Stephen F. Arno are Research Ecologist and Research Forester, Intermountain Fire Sciences Laboratory, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, P.O. Box 8089, Missoula, MT 59801.



Figure 2—Whitebark pine often is the only tree that can grow on harsh sites. Here, in the Challis National Forest in central Idaho, whitebark pine is the climax tree species.

and others 1990) (fig. 4). Large stand-replacing fires are infrequent, usually occurring only during windy conditions after prolonged drought. The fires that burned in and around Yellowstone National Park in 1988 were spectacular examples of the large, high-intensity fires that periodically burn within whitebark pine and adjacent forest types. These fires burned whitebark pine habitats in a patchy, stand-replacing manner.

During the 10,000 years since development of forests after the last glacial retreat, fires have had a major influence on the structure and composition of forests in the Northern Rocky Mountains (Arno 1980). Fire occurrence has been significantly altered by human activity. Native Americans used fire to manipulate vegetation, for hunting, for communication, and for other purposes (Pyne 1982). More recently, humans have affected fire occurrence by purposefully or inadvertently igniting fires, through fire suppression, and by grazing domestic livestock, logging, or otherwise altering the fuels available to burn. Efforts to suppress fires have become increasingly effective since about 1935 (Arno 1980; Pyne 1982).



Figure 3—Whitebark pine trees often survive fires and individual trees may survive multiple fires. Information on fire frequency and effects is derived from dates of fire scars on tree sections such as this one from a 208-year-old whitebark pine tree in the Shoshone National Forest in northwestern Wyoming. First scarred by fires when only 12.2 cm in diameter at the base, it was again scarred 60 years later. It was cut in 1988, 110 years later.



Figure 4—Young whitebark pine trees regenerated successfully following a stand-replacement fire in northwestern Wyoming. All trees were killed by the fire, which occurred 55 years before this photograph was taken in 1988.

WHITEBARK PINE DECLINE

Whitebark pine has declined in abundance in major portions of its range (Arno 1986). Once important on 10 to 15 percent of the forested landscape in the Northern Rocky Mountains (Arno and Hoff 1989), whitebark pine mortality rates averaged 42 percent over the last 20 years in western Montana (Keane and Arno 1993). Arno and others (1993) found that for a 200-ha study area in Montana, the percentage of stands with at least 20 percent basal area of mature whitebark pine declined from 37 percent in 1900 to 20 percent in 1991; 14 percent of the area was dominated by whitebark pine in 1900; none was so dominated in 1991.

Whitebark pine decline is most pronounced on the more productive sites where subalpine fir and Engelmann spruce are highly competitive (Arno 1986; Ciesla and Furniss 1986; Keane and Arno 1993; Kendall and Arno 1990). Declining whitebark pine threatens wildlife habitat because the seeds of whitebark pine are a valuable food for many birds and small mammals, including the endangered grizzly bear (Kendall and Arno 1990).

Recent decline in whitebark pine abundance is linked to less frequent fires (Keane and Morgan, these proceedings; Keane and others 1990). Fires in whitebark pine forests occurred at mean intervals of 30 to 300 years based on fire history information derived from fire scars and stand ages (table 1). Fewer fires in the last 50 to 100 years (Arno and Hoff 1989; Morgan and Bunting 1990) have resulted in extensive changes in the composition of forests in the high-elevation landscapes of the Northern Rocky Mountains. Composition of subalpine forests has shifted dramatically toward dominance by subalpine fir and Engelmann spruce (Keane and others 1993). The decline of whitebark pine has been further exacerbated by the introduced blister rust (*Cronartium ribicola*) and the native mountain pine beetle (*Dendroctonus ponderosae*), both of which kill whitebark pine but not subalpine fir or Engelmann spruce.

STAND-REPLACING FIRES

In conditions of extreme drought lasting more than 2 years, fires ignited by lightning and fanned by high winds can rapidly spread and kill trees in large patches. These fires usually burn in other forest types as well, converting large segments of the landscape to early successional plant communities. Fires that spread through forests at lower elevations historically burned into the adjacent whitebark pine forests (Arno and Hoff 1989). In whitebark pine forests, stand-replacing fires typically spread on the ground (Lasko 1990). Fires may kill trees by scorching foliage or by heating the bole or roots to lethal temperatures. Sometimes, crown fires occur that burn through the tree crowns, killing all trees in their paths (Lasko 1990).

Stand-replacing fires provide important opportunities for whitebark pine to regenerate. Many competing tree species rely on the wind to disseminate seed. Whitebark pine has a distinct advantage in regenerating following extensive disturbances (Tomback and others 1990). The Clark's nutcracker (*Nucifraga columbiana*) commonly transports seeds several kilometers (Hutchins and Lanner 1982). These birds prefer open, burned areas for caching seeds (Tomback and others 1990). Thus, although large fires are infrequent, they are ecologically important in maintaining extensive whitebark pine forests on the landscape.

LOW-INTENSITY SURFACE FIRES

Low-intensity surface fires also influence the relative abundance of whitebark pine on the landscape. Such fires are more frequent and smaller in extent than stand-replacing fires. Low-intensity fires generally kill young whitebark pine and both large and small subalpine fir. Such fires can result in open, parklike stands of nearly pure whitebark pine (Arno 1986). Some fires probably burned as low-intensity surface fires but later became stand-replacing fires when burning conditions were more severe. That whitebark pine trees often survive surface fires is evidenced by the many living trees that have scars from one or more fires (fig. 1).

Table 1—Fire frequency from whitebark pine forests expressed as the mean and range (in parentheses) of the years between fires

Fire frequency	Geographical area and reference
144 (55 to 304)	Bob Marshall Wilderness Complex, northwestern Montana (Keane and others 1993)
80 (50 to 300)	Bitterroot Mountains, Montana (Arno 1980)
30 to 41 (4 to 78)	100- to 300-ha stands where subalpine fir is climax, Montana (Arno 1986)
29 (13 to 46)	10 stands within 100 ha, northwestern Wyoming (Morgan and Bunting 1990)
300	Lodgepole pine forests adjacent to but at lower elevations than whitebark pine, Yellowstone National Park (Romme 1982)

These low-intensity fires are more common on relatively dry sites, occurring only where stand structures, fuel accumulation, and microclimatic conditions are conducive. Thus, such fires result in many small burned patches, increasing landscape heterogeneity.

Where fires are more frequent, they are more likely to be of low intensity. Morgan and Bunting (1990) documented very frequent low-intensity fires on a relatively dry site supporting seral whitebark pine in open, parklike stands within a 100-ha area in northwestern Wyoming. There the mean interval between fires was 33 years prior to 1867. Fires were much more common prior to 1850 than they have been since then (Morgan and Bunting 1990).

FIRE REGIMES

Through time, most whitebark pine forests experience a mixture of stand-replacement and low-intensity fires. The frequency of these types of fires within a given landscape will vary with landscape complexity and heterogeneity. Stand-replacing fires are more common during regional droughts, and often burn large patches regardless of fuel loading or stand condition. Fire behavior and effects are also influenced by the stand structure and fuel accumulation, which are in part determined by the time since last burn.

Where whitebark pine is climax, fires are infrequent and generally of low intensity. In whitebark pine krummholz and ribbon forests, fires are infrequent and of variable intensity. When fires do occur, many trees die and regeneration is very slow. Keane and others (1990) predict where blister rust infection rates are high, climax whitebark pine forests will convert to herbaceous or shrub communities following fire.

Stand-replacing fires are more common where whitebark pine is a seral dominant. Stand-replacing fires become increasingly likely with advancing succession (Fischer and Clayton 1983; Morgan and Bunting 1990).

SUCCESSION FOLLOWING FIRE

Fire is a key process affecting seral whitebark pine forest structure and composition. Successional patterns on sites where whitebark pine is seral are predictable (fig. 5), but they are not closely tied to stand age or time since last disturbance (Mattson and Reinhart 1990). The stand structure and the microsites created vary from fire to fire. Conditions for successful regeneration of tree seedlings are sporadic, depending on favorable climatic and site conditions. Although both subalpine fir and whitebark pine may establish soon after a fire, it may take a half-century or longer for a forest to develop.

Whitebark pine is one of the first tree species to become established in abundance following stand-replacing fires (Weaver and Dale 1974). As a consequence, it often dominates initially, often for up to 225 years or more (Loope and Gruell 1973; Morgan and Bunting 1990). Early seral stands are dominated by whitebark pine seedlings and saplings growing along with a dense herbaceous and shrub understory. Subalpine fir seedlings are often present, especially close to parent trees that survived the fire, but they grow more slowly than whitebark pine trees (Arno

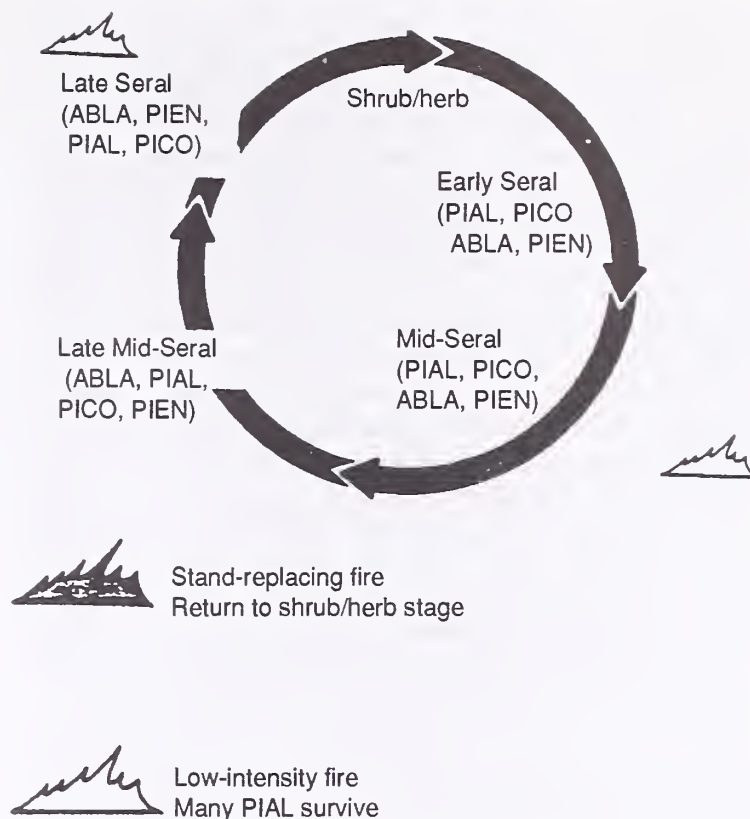


Figure 5—Generalized forest succession following fires on sites where whitebark pine (PIAL) is replaced by subalpine fir (ABLA) and Engelmann spruce (PIEN) with advancing succession. Lodgepole pine (PICO) is a common associate. Low-intensity surface fires may occur at any stage but are most likely in mid-seral stands. Stand-replacing fires are the norm in late-seral stands. Tree species listed in order of abundance. Adapted from Fischer and Clayton (1983).

and Hoff 1989). Whitebark pine seedlings are more abundant than subalpine fir seedlings in large burned areas because whitebark pine seedlings are dispersed farther by the Clark's nutcracker. Subalpine fir seeds are dispersed by the wind. Many standing snags and fallen logs are present. Most whitebark pine trees do not produce large numbers of seeds until at least age 70; most do not produce any cones until age 50 (Morgan and Bunting 1992). With time, whitebark pine is gradually replaced by subalpine fir and Engelmann spruce. In late-seral stands, both the tree canopy and the understory are dominated by many subalpine fir trees.

MANAGEMENT IMPLICATIONS

Continued decline in whitebark pine abundance threatens to dramatically reduce the availability of seeds for the many animals that rely on them as a food source (Arno 1986).

Fire exclusion greatly reduces opportunities for regeneration of whitebark pine. Cone production is higher in the stands where whitebark pine is healthy and dominant (Morgan and Bunting 1992). With blister rust reducing cone production and killing parent trees (Arno and Hoff 1989), the seed available for tree regeneration is rapidly

declining (Arno 1986; Keane and Arno 1993). As cone production declines, animals eat more of the seeds, leaving fewer to regenerate. Whitebark pine cone production declines with advancing succession (Morgan and Bunting 1992) and as infection by blister rust increases (Arno and Hoff 1989). Given the rapidly declining abundance of whitebark pine in some regions, we must act quickly to create opportunities for individuals that are resistant to blister rust to regenerate. Although whitebark pine is very sensitive to blister rust, some individual trees are genetically resistant to infection (Hoff and others 1990). If we do not create opportunities for those trees to regenerate before their cone production declines or they die in advancing succession, opportunities for enhancing natural mechanisms of whitebark pine recovery will be lost.

Three options are available for improving the health and productivity of whitebark pine stands that are now dominated by subalpine fir and spruce. One option is creating forest openings through timber harvest, girdling, or otherwise killing trees mechanically. Cutting trees to create openings to encourage regeneration of whitebark pine is possible but may not be economically feasible. Although there are often small whitebark pine trees growing in the understory of mixed conifer stands, they are often very old and of poor vigor and are therefore unlikely to respond when larger trees are removed.

Another option is the liberal use of prescribed fire to create openings for regeneration and to favor whitebark pine in stands now codominated by subalpine fir. Managers can purposefully ignite fires or allow lightning fires to burn under carefully prescribed conditions of weather, fuel, and location. Historically, fire was the primary natural disturbance, and it may be the most practical tool for managing whitebark pine considering economics, policy, and topographic limitations for using timber harvest.

A third option, to use a combination of techniques, may be most successful. Arno and Keane are involved in an effort to test alternative techniques for perpetuating whitebark pine in a blister rust-infected area of the Bitterroot National Forest in Montana.

ACKNOWLEDGMENTS

Research funding was provided through the USDA Forest Service, Intermountain Research Station. This is Contribution No. 693 of the Idaho Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID 83843. We thank Bill Fischer and Elizabeth Reinhardt for their comments.

REFERENCES

- Arno, S. 1980. Forest fire history in the Northern Rockies. *Journal of Forestry*. 78(8): 460-465.
- Arno, S. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-94.
- Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.
- Arno, S. F.; Reinhardt, E. D.; Scott, J. H. 1993. Forest structure and landscape patterns in the subalpine lodgepole pine types: a procedure for quantifying past and present conditions. Gen. Tech. Rep. INT-294. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 17 p.
- Ciesla, W. M.; Furniss, M. M. 1986. Idaho's haunted forests. *American Forests*. 81(8): 23-25.
- Fischer, W. C.; Clayton, B. D. 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. Gen. Tech. Rep. INT-141. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 83 p.
- Hoff, R. J.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. *European Journal of Forest Pathology*. 10: 307-316.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Keane, R. E.; Arno, S. F. 1993. Rapid decline of whitebark pine in western Montana: evidence from 10-year measurements. *Western Journal of Applied Forestry*. 8(2): 44-47.
- Keane, R. E.; Arno, S. F.; Brown, J. K.; Tomback, D. F. 1990. Modelling stand dynamics in whitebark pine forests. *Ecological Modelling*. 51: 73-95.
- Keane, R. E.; Morgan, P.; Menakis, J. 1993. Landscape assessment of the decline of *Pinus albicaulis* in the Bob Marshall Wilderness Complex, Montana, USA. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory. Review draft.
- Kendall, K. C.; Arno, S. F. 1990. Whitebark pine—an important but endangered wildlife resource. In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 264-273.
- Lasko, Richard J. 1990. Fire behavior characteristics and management implications in whitebark pine ecosystems. In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 319-323.
- Loope, L. L.; Gruell, G. E. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quaternary Research*. 3: 425-443.
- Mattson, D. J.; Reinhart, D. P. 1990. Whitebark pine on the Mount Washburn Massif, Yellowstone National Park. In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 106-117.
- Morgan, P.; Bunting, S. C. 1990. Fire effects in whitebark pine forests. In: Schmidt, W. C.; McDonald, K. J., comps.

- Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 166-170.
- Morgan, P.; Bunting, S. C. 1992. Cone crops in whitebark pine (*Pinus albicaulis*) forests in the Greater Yellowstone Area. Moscow, ID: University of Idaho, College of Forestry, Wildlife and Range Sciences. 21 p. Review draft.
- Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.
- Pyne, S. J. 1982. Fire in America. Princeton, NJ: Princeton University Press. 654 p.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs. 52: 199-221.
- Steele, R.; Pfister, R. D.; Ryker, R. A.; Kittams, J. A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 138 p.
- Steele, R.; Cooper, S. V.; Ondov, D. M.; Roberts, D.; Pfister, R. D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.
- Tomback, D. F.; Hoffman, L. A.; Sund, S. K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-130.
- Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation and production. American Midland Naturalist. 92: 222-230.

VEGETATION DISTRIBUTION AND PRODUCTION IN ROCKY MOUNTAIN CLIMATES—WITH EMPHASIS ON WHITEBARK PINE

Tad Weaver

Abstract—The distribution and production of vegetation on the altitudinal gradient (grassland-forest-alpine) was plotted against climatic parameters to evaluate hypothetical controlling factors. (1) Whitebark pine (*Pinus albicaulis*) is likely excluded from higher zones by a cool growing season or wind-induced drought. It is probably not excluded by low temperatures occurring during its hardening, hard, or dehardening seasons. (2) While the lower physiological limit of whitebark pine is probably set by drought, its lower realized limit is directly set by subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*) competitors and indirectly set by factors that control their distribution. (3) The upper limits for most other dominant species are probably set by growing season temperature. The lower limits are likely set by competition down to the cedar-hemlock (*Thuja plicata*/*Tsuga heterophylla*) zone and by drought in drier areas. (4) Production is strongly correlated ($r^2 = 0.86$) with growing season length (soil thawed season minus dry soil days). Multiplying season length by average temperature did not improve the growing season predictor, perhaps because vegetation at each altitude is especially adapted to temperatures in its zone.

Vegetation composition and structure vary along gradients of temperature and precipitation whether the condition changes with altitude (Daubenmire 1956; Gams 1931; Weaver 1980) or geography (Holdridge 1967; Walter 1973; Whittaker 1975). Graphical devices based on simple parameters such as average annual temperature and total annual precipitation (Holdridge 1967; Whittaker 1975) are workable predictors of the vegetation growing in particular climates. It seems obvious, however, that these devices succeed, not because the climatic parameters used are causal, but because the parameters are correlated with causal climatic factors.

Production of vegetation is largely determined by climate and is therefore expected to be highest where temperature, moisture, and nutrients are simultaneously favorable. In Rocky Mountain vegetation one therefore expects production to be highest in low-altitude (warm) moist forests (*Thuja-Tsuga*) and to decline both with increasing altitude (because of cooling and reduced nutrient availability) (Weaver 1979) and with decreasing altitude (because of decreasing water availability). While it is

rarely done, vegetation production should also be successfully plotted in a Hutchinsonian (1958) hyperspace with axes that are either physiologically meaningful or surrogates well correlated with physiologically meaningful axes.

The object of this paper is to correlate vegetation performance—survival and production—with physiologically meaningful aspects of temperature and moisture. Study of the distribution of species on these presumptively causal axes will eliminate some hypotheses of cause and sharpen others for experimental tests. While whitebark pine (*Pinus albicaulis*) is the primary subject of this paper, the approach could be applied to other species, as well.

METHODS

Impacts of climatic factors on vegetation distribution were evaluated by comparing factor levels among segments on a vegetational gradient. In essence, the method allows one to deduce (1) that a presumptive factor that does not vary between vegetation types is not controlling the vegetation changes observed, and (2) that a presumptive factor that does change between vegetation types deserves further discussion as directly controlling, indirectly controlling, or a noncausal correlate. The method is illustrated here with discussion of whitebark pine, but it could be applied to many other species as well.

The Data

Environmental zones were identified by climax vegetation occupying them (Daubenmire 1943; Daubenmire and Daubenmire 1968; Huschle and Hironaka 1980). They included, from low to high altitude, desert shrub, dry grassland, warm forest, cool forest, and alpine ecosystems. Specific zones are listed with their Kuchler (1964) type numbers and representative stations in table 1.

Climates of the environmental zones were characterized by using climatic statistics from approximately five stations in each environmental-vegetation zone. To maintain the integrity of the data, raw data are plotted wherever possible. When necessary, medians were used to represent "typical" sites; use of medians deemphasizes sites with conditions intermediate between modal conditions of adjacent types. The stations chosen include most available stations and may thus be considered as a "complete sample." The sample may not be entirely random because weather stations must be accessible; in higher types, for example, the sites may be relatively low.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Tad Weaver is Plant Ecologist, Biology Department, Montana State University, Bozeman, MT 59717.

Table 1—Weather stations representative of major Northern Rocky Mountain environmental zones.¹ Zones are listed from high to low altitude

Zone	Station locations
Alpine ²	White Mountain, CA; Niwot Ridge, CO
Whitebark pine ²	Old Glory, BC; Kings Hill, MT; Ellery Lake, CA; Crater Lake, OR
Subalpine fir	High: Summit, MT; West Yellowstone, MT; Lake Yellowstone, MT; Low: Burke, ID; Seeley Lake, MT; Hungry Horse, MT
Douglas-fir	East: Hebgen Lake, MT; Lakeview, MT; Lamar, WY; Palisades Dam, ID; Dixie, ID; West: Libby, MT; Lincoln, MT
Cedar-hemlock	West Glacier, MT; Sandpoint, ID; Pierce, ID; Avery, ID; Priest, ID
Ponderosa pine	West: Garden Valley, ID; Polson, MT; Potlatch, ID; Kooskia, ID; East: Melstone, MT; Busby, MT; Colstrip, MT; Lame Deer, MT; Roundup, MT
Idaho fescue	Gallatin Gateway, MT; Virginia City, MT; Mystic Lake, MT; Wisdom, MT; Bozeman MSU, MT; White Sulphur Springs, MT
Bluebunch wheatgrass	Browning, MT; Belgrade, MT; Kalispell, MT; Ennis, MT; Dillon, MT; Augusta, MT; Crow Agency, MT; Billings, MT
Grama grass	Ekalaka, MT; Jordan, MT; Malta, MT; Rock Springs, MT; Rapelje, MT; Chester, MT; Great Falls, MT; Fairfield, MT
<i>Atriplex</i> spp.	Lovell, WY; Worland, WY; Basin, WY; Powell, WY; Deaver, WY

¹The vegetation types, with their Kuchler (1964) type numbers (KTXX), are: *Deschampsia caespitosa*-*Carex* (KT52), *Pinus albicaulis* (KT15), *Abies lasiocarpa* (KT15), *Pseudotsuga menziesii* (KT12), *Thuja plicata*/*Tsuga heterophylla* (KT2), *Pinus ponderosa* (KT11,16), *Festuca idahoensis* (KT63), *Agropyron spicatum* (KT63), *Bouteloua gracilis* (KT64), *Atriplex* (KT40). *Abies* types from higher and lower altitudes, *Pseudotsuga* types from east and west of the mountains, and ponderosa pine types from east and west of the Rockies are separately presented to emphasize possible differences.

²The White Mountain alpine site (10,150 ft) is unusually dry. The Ellery Lake whitebark pine site has only precipitation data; temperature data were therefore taken from a similar altitude at a nearby White Mountain site (9,645 ft).

Killing Temperatures

The hypothesis that extreme temperatures might exclude a plant (for example, whitebark pine) from an adjacent zone was tested by determining whether the condition is more extreme in the unoccupied than in the occupied zone; if it is not, the hypothesized factor is considered unlikely to be lethal. This test was used on temperatures of early fall frosts, midwinter extreme lows, midwinter average lows, late fall frosts, midsummer average highs, and midsummer extreme highs. Midwinter lows and midsummer highs were tested because these temperatures might exceed the potential tolerances of a plant; fall and spring frosts were considered because they might kill partially hardened plants. Fall frost temperatures were measured as the absolute low in the month in which average temperature first fell below 0 °C; where no month had an average temperature of 0 °C, the values were interpolated to 0 °C from adjacent months. Spring frost temperatures were estimated similarly for the month in which average temperatures first rose above 0 °C. I argue later (see growing season) that average temperatures below 0 °C restrict water and nutrient uptake and therefore open and close the growing season; the use of 0 °C is in contrast to the 5 °C used by many phenologists (for example, Chang 1968). "Absolute" temperatures were the lowest (or highest) seen in the period of record—10 years or more.

Starvation Temperatures

The plant might be excluded from a zone free from killing events if (temperature) conditions failed to support net photosynthesis on an annual basis. Two indices of growing season temperature were used to test the possibility of such starvation. First, temperatures were averaged across all growing season (defined later) months. Despite its common use in predicting growth (Chang 1968; Larcher 1975), this index is expected to underestimate the

benefits of warmer temperatures because chemical reaction rates increase exponentially with increasing temperature. An alternate index of temperature was therefore tested. In the second index temperatures were replaced with growth support units (gsu) and these were averaged across the season. On the assumptions that $Q_{10} = 2$, that very slow growth begins at 1 °C, and that native plants tolerate normal high temperatures of their zones, the growth support unit curve was constructed by interpolating between 0 growth rate units (gsu) at 0 °C, 1 gsu at 1 °C, 2 gsu at 11 °C, 4 gsu at 21 °C, 8 gsu at 31 °C, and 16 gsu at 41 °C. That is, we expect no growth at 0 °C or below, 1 unit at 1 °C, 2 units at 11 °C, 4 units at 21 °C, etc.

Killing Drought

Evaporation equals roughly 2 mm/°C × month (Daubenmire 1956; Nielson 1986; Stephenson 1990; Thornthwaite 1948; Walter 1973). As a result, one might index drought duration by counting months when average precipitation (mm/2) is less than average temperature (C) or drought intensity by summing, across growing season months, precipitation deficits below the calculated balance.

A count of months registering drought on the Walter index may overestimate drought duration where the deficit is small because drought may open late or close early in the month. To minimize this effect I have normalized drought duration from a scatter diagram of duration against deficit: 0-5 mm = 0 months, 6-15 mm = 1 month, 16-35 mm = 2 months, 36-50 mm = 3 months, and 51-85 mm = 4 months.

I have used the sum of warm-season (average temperature above 0 °C) water deficits as an index of drought magnitude. I do so with the recognition that, due to exclusion of important factors (for example, wind, Penman 1949, and exponential temperature effects, Stephenson 1990), this index usually underestimates water deficit.

Water Starvation

"Water starvation" should occur where plants are not desiccated, but where water supplies do not support net photosynthesis on an annual basis. For example, starvation would occur if water were continually available, but evapotranspiration equaled or exceeded uptake rates. Such starvation would select for organisms with lower ET rates: Mesophytic leaves would be replaced by xerophytic leaves and leaf exposure might be reduced by reduction of stature even to the point where plants existed only at the ground surface or under transparent rock.

Growing Season

For sensitive introduced plants, frost-free season is often recorded as an indicator of season length (Burke and others 1976; USGS 1971).

Since cool region plants normally tolerate growing season frosts, I argue for a different index. Growth requires both leaf activity (photosynthesis) and root activity (water and nutrient absorption). For plants with frost-insensitive leaves (Burke and others 1976), midday temperatures should be high enough for photosynthesis long before soils are thawed. Root activity extends (maximally) from spring soil thaw to the fall refreeze, so this period should be a better index of growing season length. Thus I open and close the growing season with 0 °C average monthly air temperatures. So represented, initial activity in grasslands begins at spring soil temperatures (0-25 cm) near 0 °C and activity ceases in the fall with soil temperatures as high as 5 °C (Weaver, in preparation). In, or adjacent to, the subalpine fir (*Abies lasiocarpa*) zone the growing season may exceed this period because deep snow cover may prevent the freezing of soil water.

While the temperature-bounded season probably applies at high-altitude sites, at low-altitude sites soil drying may close the growing season before frost does. Thus, one may better index growing season as warm season months minus any drought months included in the warm season. While the Northern Rocky Mountain drought season comes at summer's end (Weaver 1980), this index will also apply to regions where the warm season opens with dry months. It is conceivable that other periodic factors, for example nutrients or pest attack, might affect growing season length.

Production

Production estimates for each series were drawn from the literature (table 2). These are correlated with climatic conditions that might control them: warm season length, warm moist season length, and the product of warm soil season length and temperature. For the latter, two temperature expressions were tested: average temperature minus 5 °C and Q_{10} (the Q_{10} -based average). The third (product) indices were expected to be best because they assume that plants grow when soils are unfrozen-moist and that their growth rate is proportional to temperature (over 5 °C for the first linear index and over 1 °C for the second exponential index).

RESULTS AND DISCUSSION

In the Northern Rocky Mountains vegetation changes from grass-shrub (*Atriplex*, *Bouteloua*, *Agropyron*, and *Festuca*) to conifer (*Pinus ponderosa*, *Thuja-Tsuga*, *Pseudotsuga*, and *Abies*) to alpine graminoid with increasing altitude. Subzones listed parenthetically are described by Daubenmire (1943) and mapped by Kuchler (1964). This paper compares weather data gathered in these zones to test hypothesized controls of distribution and production. The method is illustrated with whitebark pine.

Upward Limits

I speculate that the upward limits of whitebark pine might be determined by lethal factors (winter low temperatures, spring-fall frosts, or desiccation) or production deficits (starvation) due to inadequate water or heat units. These hypotheses are considered in the following paragraphs.

If winter lows are lower in the alpine than in the pine zone below, winter cold might be the excluding factor, otherwise not. Contrary to my expectation, neither absolute lows nor average January minima are lower in the alpine than in the pine (or most other) vegetation zone(s) (fig. 1). The failure of low temperatures to develop at higher altitudes may be due to the high density of cold air: Cold air entering from the north stays low like mercury poured under water and air cooled by exposure to cold alpine ground runs off (Geiger 1965). Since extreme temperatures are not lower at high than low altitude, I deduce that neither whitebark pine, nor most other native dominants, are excluded from high sites by extreme low temperatures of winter. An exception to this generalization seems to appear in high- or low-altitude frost pockets, where accumulating cold air may kill trees in winter or spring (Weaver 1990).

For natives of an area, I suggest that frost damage is more likely when plants are partially hardened (fall) or partially dehardened (spring) than at midwinter. I expect (1) winter to be delimited approximately by the fall month in which surface soils fall below 0 °C and the spring month in which they rise above 0 °C, (2) winter to be a season of low root activity, low water, and low nutrient uptake, and (3) 0 °C soil temperatures to be approximately coincident with 0 °C air temperatures (Weaver, in preparation). I therefore (1) compare, across vegetation types, observed temperature lows in these spring-fall seasons of incomplete frost hardness (fig. 2), (2) discover no difference, and (3) conclude that frosts probably do not partition vegetation native to the region. The preceding discussion depends on the assumption that plants harden and deharden in phase with air/soil temperatures. This argument would be fallacious if day length were the primary controller of the hardening/dehardening process. However, since both temperature and correlated day length triggers are important (Salisbury and Ross 1992), I expect frosts to exclude plants from environmentally distant, but not environmentally adjacent, vegetation types.

While frosts and winter freezes probably do not exclude whitebark pine from the alpine (or other plants from the vegetation zone immediately above), a lack of heat units

Table 2—Productivity in grams per square meter per year and aboveground standing crop (Abvegr std crp) of major Rocky Mountain vegetation types

Vegetation type	Productivity ²	Abvegr std crp	Source
	<i>g/m²/yr</i>	<i>t/ha (age, yr)</i>	
Alpine	135 100-200	1.35 1.00-2.00	Thilenius and others 1974 Scott and Billings 1964
<i>Pinus albicaulis</i>	¹ 60 ¹ 25-75 (53) 200-700	¹ 140 (300-500) 350 (300-500)	Weaver and Dale 1974 Pfister and others 1977 Forcella and Weaver 1977
<i>Abies lasiocarpa</i>	100-200 860 ¹ 95-180 (137)	160 (300-700) 357 (106 yr) 100-250 (old) 150-250	Aplet and others 1989 Whittaker and Niering 1975 Pfister and others 1977 Weaver and Forcella 1977 Landis and Mogren 1975
<i>Pseudotsuga menziesii</i>	1,550 ¹ 30-170 (150)	438 (252) 100-350 (350+)	Whittaker and Niering 1975 Pfister and others 1977 Weaver and Forcella 1977
<i>Thuja plicata</i> - <i>Tsuga heterophylla</i>	870 550 1,380 ¹ 150-330 (240)	290 (105) 316 (250) 504 (103) 	Hanley 1976 Hanley 1976 Hanley 1976 Pfister and others 1977
<i>Pinus ponderosa</i>	¹ 188 ¹ 30-150 (188) 490-570	 150-250 (150) 50-250 (350+)	Clarey and others 1975 Pfister and others 1975 Whittaker and Niering 1975 Weaver and Forcella 1977
<i>Festuca idahoensis</i>	235 195 147	2.35 1.95 1.47	Collins and Weaver 1978 Weaver and Collins 1977 Daubenmire 1970
<i>Festuca scabrella</i>	152	1.52	Willms and others 1986
<i>Bouteloua gracilis</i>	103 53-95	1.03 0.5-1.0	Weaver 1983 Hunt and others 1988
<i>Atriplex</i> spp.	28		West 1983

¹Since merchantable production and standing crop are emphasized in these studies, one might expect the figures to be 50 to 66 percent of those reported in studies of total production (Weaver and Forcella 1977).

²Where production and standing crop are expressed volumetrically, masses were calculated using specific gravities of ABLA=0.38, PIAL=0.40, PIEL=0.35, PSME=0.45, PIPO=0.43, PICO=0.38, THPL=0.33, TSHE=0.41 (U.S. FPL 1974).

(starvation) may exclude, from an altitudinal zone, plants of lower zones. Average growing season temperatures in the alpine (and for most zones below it) are distinctly lower than temperatures in the vegetation zone below (fig. 3). This correlation suggests the possibility of—but does not prove—significant effects of growing season temperature. In support of this hypothesis, production-temperature relations (discussed below) suggest that the vegetation of each altitudinal zone is especially adapted to temperatures occurring in its zone. In this regard, it is satisfying to see that optimum temperatures for whitebark pine photosynthesis (20-25 °C, Jacobs and Weaver 1990) are similar to summer maximum temperatures (10-25 °C, Weaver 1990).

Graphs of estimated soil water availability against vegetation type (fig. 4) indicate little or no stress in alpine, whitebark, subalpine fir, and Douglas-fir zones. On this basis one might exclude drought as a factor determining whitebark's upslope limit. Due to two modifying factors,

this conclusion seems premature. First, as one moves upslope from forest to alpine (or mountain meadow), winds increase and, with increasing wind, drought increases due to reduced water availability—snow may be blown off site (Daubenmire 1981) and water in uninsulated soils freezes—and increasing water loss—through abrasion of cuticle (Hadley and Smith 1987) and thinning of the leaf's boundary layer (Gates and Papian 1971; Nobel 1983). I see winter wind effects as probable controllers because trees invading (or planted into) mountain meadows are more often desiccated in winter than summer. The wind effect hypothesis is consistent with the fact that groups of trees sometimes invade sites that individuals cannot invade alone (Armand 1992; Tranquillini 1979). In such situations adjacent trees are more likely sheltering each other from drying wind than from lethal low temperatures. Second, as one moves upslope the average soil becomes progressively better drained (Weaver 1979), and thus effective precipitation is a smaller fraction of total

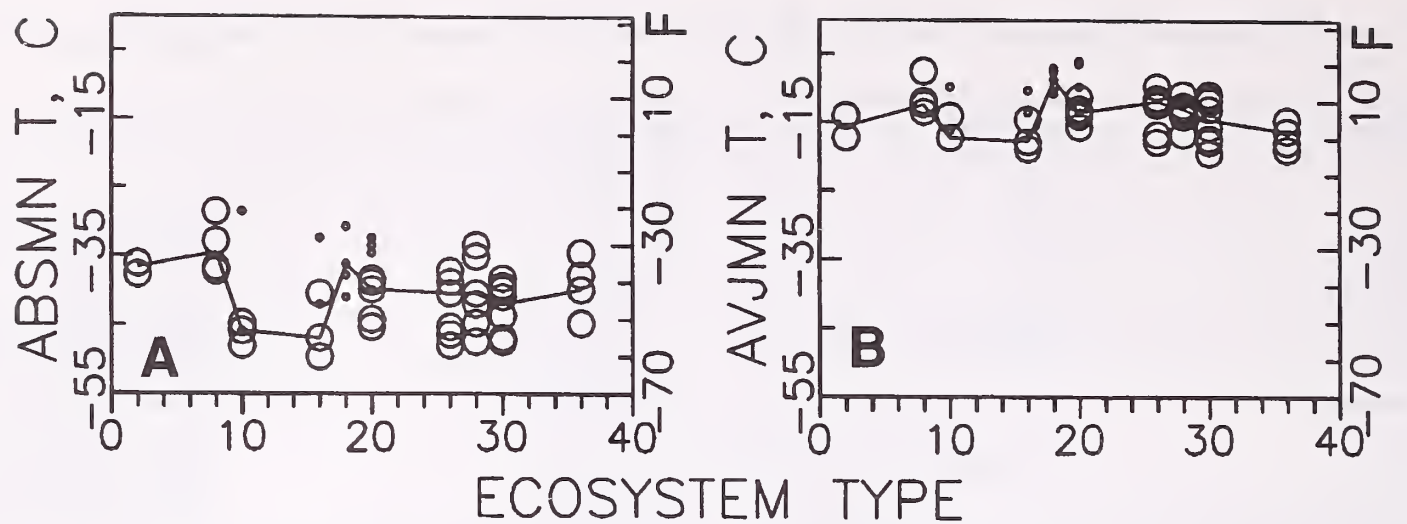


Figure 1—Midwinter low temperatures in 10 Rocky Mountain ecosystems. Low temperatures ($^{\circ}\text{C}$ and $^{\circ}\text{F}$) are represented by absolute winter minimums (A, ABSMN) and average January minima (B, AVJMN). Ecosystem types range altitudinally from alpine (2), down through forests (8-20) to grass and shrublands (26-36); specifically, they are alpine (2), whitebark pine (8), subalpine fir (10), Douglas-fir (16), cedar-hemlock (18), ponderosa pine (20), Idaho fescue (26), bluebunch wheatgrass (28), gramagrass (30), and desert shrub (36). Large and small circles represent data gathered east and west of the Rockies, respectively. Lines connect median values.

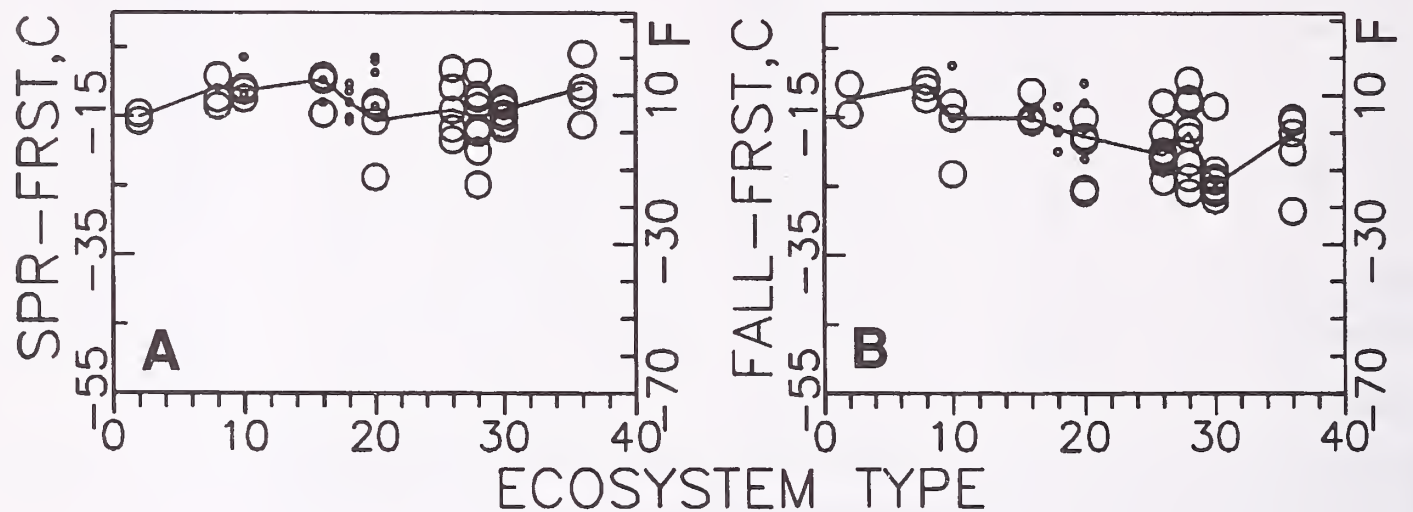


Figure 2—The coldest early spring (A, SPR-FRST) and late fall (B, FALL-FRST) frosts ($^{\circ}\text{C}$ and $^{\circ}\text{F}$) in 10 Rocky Mountain ecosystems. Ecosystems, symbols, and lines are as in figure 1.

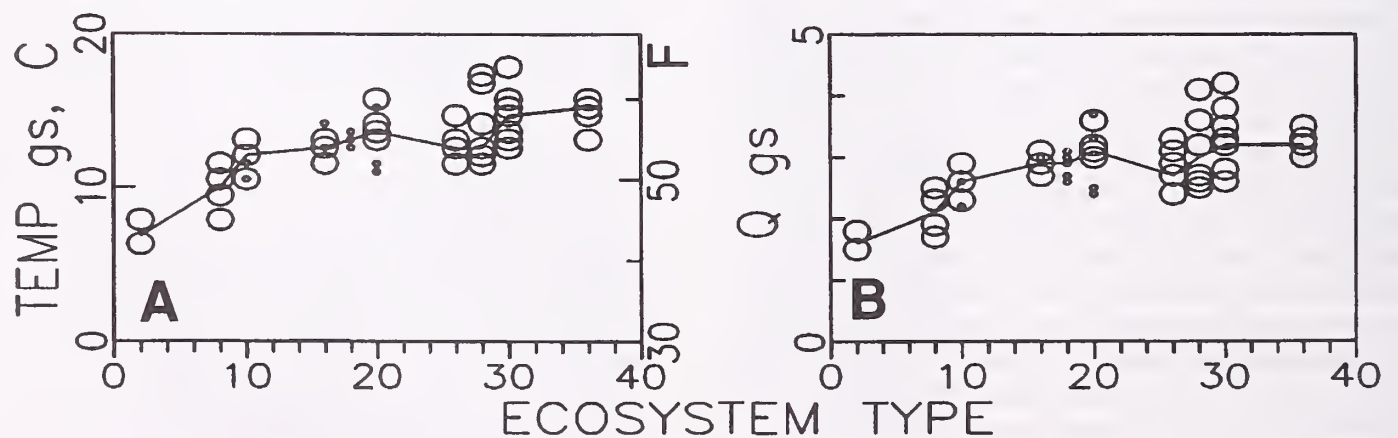


Figure 3—Average growing season temperatures in 10 Rocky Mountain ecosystems. The first graph (A, TEMP gs) gives the average growing season temperature ($^{\circ}\text{C}$ and $^{\circ}\text{F}$). Q gs in the second graph (B) considers the exponential response of physiological processes to increasing temperature (Q_{10}). Ecosystem types, symbols, and lines are as in figure 1.

precipitation at higher than lower altitudes; that is, the Walter drought indices presented in figure 4 probably overestimate water availability on (high-altitude) thin-soil sites.

Downward Limits

I speculate that downward limits of whitebark pine might be determined by heat, drought, or competition. The following paragraphs consider these hypotheses.

As one moves downslope maximum temperatures (fig. 5) rise. That this correlate of tree disappearance is not controlling is suggested by three facts. Summer averages in vegetation zones below whitebark pine (10-15 °C,

fig. 3) are well below the whitebark pine optimum (20-25 °C, Jacobs and Weaver 1990), so downward migration might actually improve production. July maxima (20-27 °C, fig. 5) in zones below are near the whitebark pine optimum temperature (20-25 °C, Jacobs and Weaver 1990) and thus should not be damaging. Long-term maxima (30-42 °C, fig. 5) in zones below do not eliminate net photosynthesis (Jacobs and Weaver 1990) and thus are probably not lethal. In addition, if whitebark pine trees are well watered, they grow well as lawn trees in the *Agropyron spicatum* zone (for example, Belgrade, MT) where temperatures are far higher than those found on sites whitebark naturally occupies.

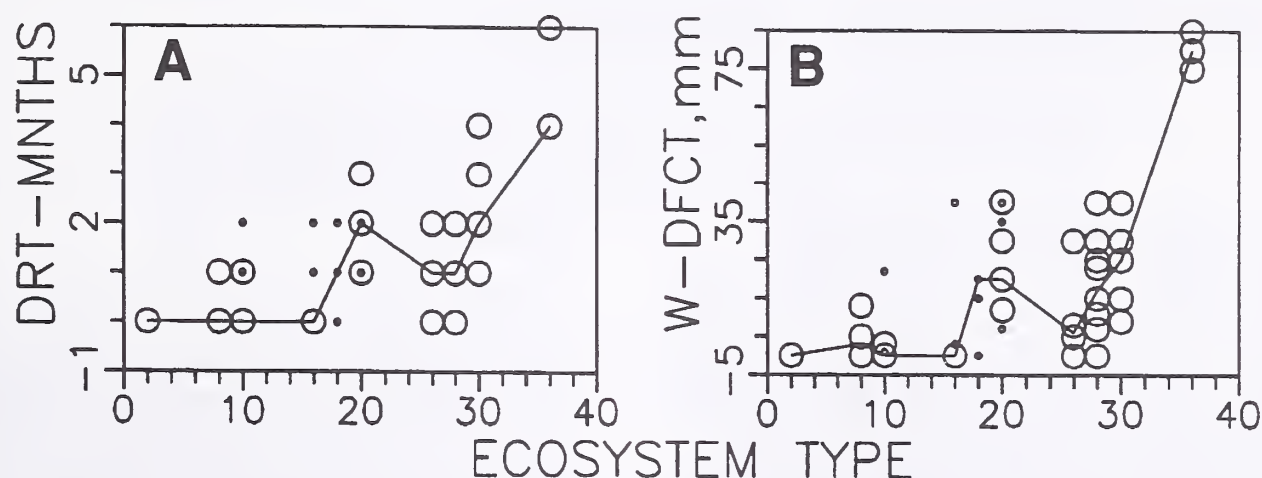


Figure 4—Drought severity in 10 Rocky Mountain ecosystems. The first graph (A) gives the number of dry months (DRT-MNTHS). The second (B) indexes the annual water deficiency (W-DFCT, mm). Both were calculated after Walter (1973). The ecosystem types, symbols, and lines are as in figure 1.

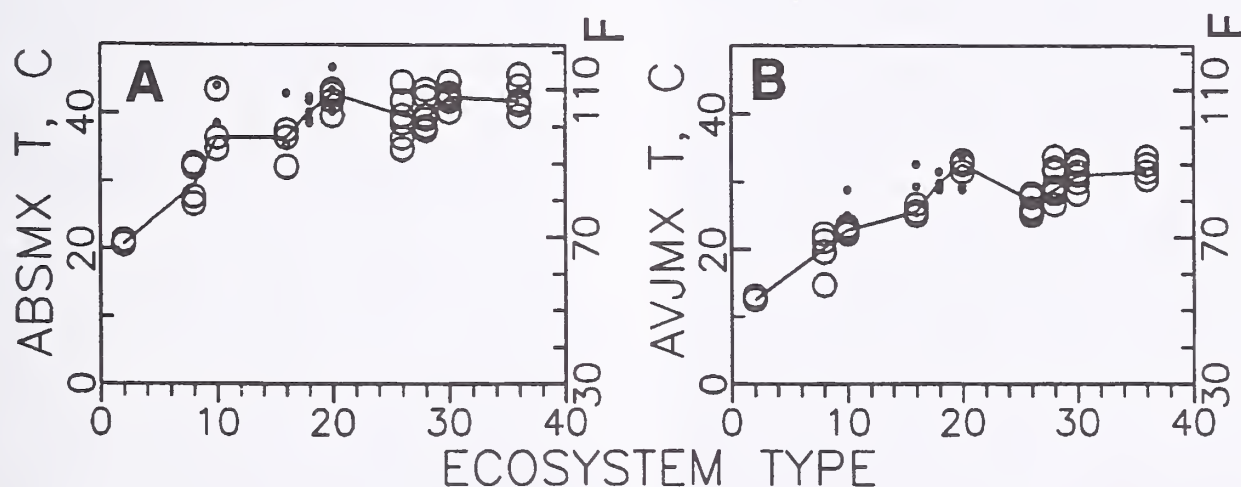


Figure 5—High temperatures (°C and °F) recorded in 10 Rocky Mountain ecosystems. The first graph (A) represents absolute summer highs (ABSMX). The second (B) gives average July maxima (AVJMX). The ecosystem types, symbols, and lines are as in figure 1.

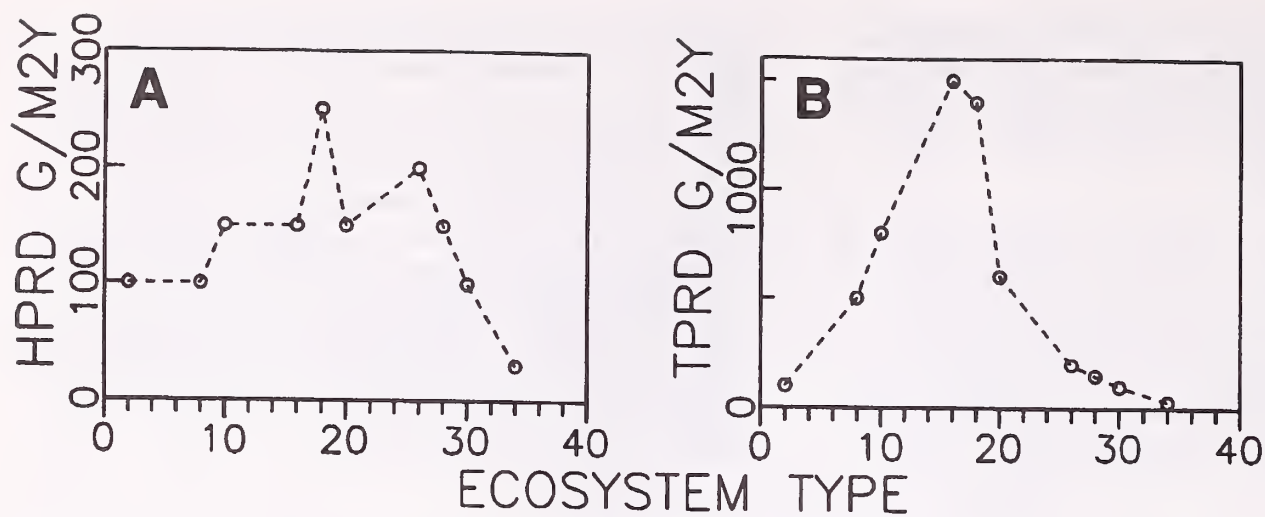


Figure 6—Biomass production in 10 Rocky Mountain ecosystems (see also table 2). The first graph (A) presents harvestable production (HPRD, g/m²/yr). The second (B) gives total production (TPRD, g/m²/yr). The ecosystem types, symbols, and lines are as in figure 1.

Drought likely sets the lower physiological limit (Hutchinson 1958) for whitebark pine's downward extension. Walter's (1973) index suggests the drought months and water deficits are near zero in high forests (whitebark pine, subalpine fir, and Douglas-fir), greater in ponderosa pine forests and grasslands, and still greater in *Atriplex* shrublands (fig. 4). If (as noted above) wind decreases and waterholding capacity of soils increases downslope, water conditions for whitebark production improve as one moves downslope; this is consistent with the fact that whitebarks growing in the subalpine fir zone can be stately timber producers (Pfister and others 1977; Weaver and Dale 1977). Water deficits remain slight down through the subalpine fir and possibly the Douglas-fir zones. The complete absence of whitebarks in the ponderosa pine and grassland zones, despite possible nutcracker dispersal (Lanner 1990; Tomback and others 1990), supports my doubt that the tree is capable of growing in the ponderosa pine and drier grassland-desert zones. Similarly, in the geographic dimension, the southern and eastern limits of whitebark pine seem to appear where precipitation in its altitudinal zone becomes too low (Arno and Weaver 1990).

The lower realized limit (Hutchinson 1958) of whitebark is set by competition with subalpine fir and lodgepole pine rather than drought. In our region, evidence for this fact lies in the tree's existence and good growth on sites in the subalpine fir zone (but apparently not in the Douglas-fir zone) where subalpine fir and lodgepole competition have been removed by clearcutting or fire. The lower limit of whitebark is, then, set by those factors—likely drought (thin soils and wind) and low summer temperature—that exclude subalpine fir and lodgepole pine from higher sites. In the geographic dimension, to the north and west where rainfall is higher, whitebark is also unable to form pure stands or disappears (Arno and Weaver 1990). (European foresters ask why we don't eliminate competitive "natives" [subalpine fir and lodgepole pine] from their zone to allow expansion of whitebark pine and increased production of quality white pine lumber.)

Production

As one moves from dry grasslands to moist forests and upward to alpine sites one sees production rise and fall again. Harvestable production—merchantable standing crop divided by years in its production—rises from dry grasslands (100 g/m²/yr) to moist forests (300 g/m²/yr) and falls through high forests to the alpine (100 g/m²/yr, fig. 6, table 2). Available data suggest that total aboveground production (total increment g/m²/yr) also increases from dry grass and shrublands (50-100 g/m²/yr) to warm forests (over 500 g/m²/yr) and falls to the alpine (100 g/m²/yr, fig. 6, table 1). The trend is parallel, but—at least in forests—total production is far higher than harvestable production. Three factors may contribute to this difference: (1) Much of the production, over the life of a stand, is lost to needle drop, self pruning, and natural thinning; this material decomposes and is recycled. The total production rates reported are deceptively high because they include nutrients being recycled to the atmosphere and soil; that is, this production consists of an actual production component based on nutrient import (weathering and atmospheric delivery) and a restructuring component based on recycling of nutrients from "obsolete" leaves, branches, and trees. (2) Only 33 to 50 percent of the material extant at harvest is merchantable (Weaver and Forcella 1977). (3) Most of the total production data comes from areas outside our region. If the climates of Douglas-fir, cedar-hemlock, and ponderosa pine stands from which production data are reported are moister or warmer than the Montana stands in which the harvestable productivity data were gathered, somewhat higher productivities might be expected.

I expect productivity to be controlled, like vegetation distribution, by climate. In the following paragraphs I will explore the hypothesis that production depends on growing season length and the warmth of that season.

Growing season length might be indexed as the number of months where daily average temperatures are above

Table 3— Relationship of production (g/m²/yr) to climatic factors

Harvestable production ¹							
HP	=	66.00	+	12.8000	WS	$p = 0.50$	$r^2 = 0.05$
		-171.00	+	70.0000	GS	$p = 0.00$	$r^2 = 0.86$
		34.00	+	1.7700	GSx T	$p = 0.04$	$r^2 = 0.44$
		-38.00	+	14.4000	GSx Q	$p = 0.01$	$r^2 = 0.58$
Log HP	=	0.78	+	0.3000	WS	$p = 0.00$	$r^2 = 0.78$
		1.75	+	0.0060	GSx T	$p = 0.12$	$r^2 = 0.27$
		1.44	+	0.0530	GSx Q	$p = 0.03$	$r^2 = 0.44$
Total production ²							
TP	=	-880.00	+	321.0000	GS	$p = 0.16$	$r^2 = 0.22$
		50.00	+	8.3200	GSx T	$p = 0.32$	$r^2 = 0.12$
		-398.00	+	77.0000	GSx Q	$p = 0.19$	$r^2 = 0.20$
Log TP	=	0.40	+	0.4700	GS	$p = 0.03$	$r^2 = 0.45$
		1.96	+	0.0086	GSx T	$p = 0.32$	$r^2 = 0.12$
		1.47	+	0.0820	GSx Q	$p = 0.22$	$r^2 = 0.22$

¹Harvestable production (HP, top diameter greater than 10 cm) and the log of harvestable production (log HP) are regressed against warm season (WS), warm-moist growing season (GS), the product of warm-moist growing season and average growing season temperature (GSxT), and the product of warm-moist growing season and Q_{10} -based growth support units (GSxQ).

²Total production (TP) and log total production (log TP) are also regressed against GS, GSxT, and GSxQ.

0 °C. The rationale is that, unless air temperatures are above 0 °C, exposed soils will be frozen (Weaver, in preparation) and frozen soils will deliver little water and nutrients. Because a regression of production against this index of growing season is so loose ($r^2 = 0.05$, table 3, fig. 7), the hypothesis that warm-season length controls production is inadequate.

The previous index may fail because, at least at lower altitudes, growing season is limited in late summer by a lack of soil water, rather than temperature. If so, the growing season index would be improved as an index of production by subtracting soil-dry months from total soil-warm months. As above, I index drought as periods when precipitation (mm/2) is less than average temperature (C, after Walter 1973). Regressions of production against months without either temperature or moisture stress explain most of the variance in harvestable production ($r^2 = 0.86$, table 3, fig. 7). Season length is a weaker correlate of total production ($r^2 = 0.22$). I offer two unsatisfying hypotheses for this important difference: (1) Growing season predicts harvestable production better than total production because photosynthates are allocated first to canopy maintenance (so this component does not vary much among types) and second to supporting structure; if so, the relationship between season length and trunk production is clarified by omitting the common leaf-twig production. (2) If total production were measured in slightly more favorable segments of the environmental types than harvestable production, the understatement of season length would weaken the relationship.

If all vegetation—grassland to forest to alpine—had a single temperature response curve, we would expect production in “warm moist soil days” to rise exponentially with increasing temperature. This expectation is based

on the rise in chemical reaction rates with rising temperature, on the resultant physiological response curves (Larcher 1975), on degree-day prediction of plant phenology (Chang 1960), and on the prediction that degree-day formulae might be improved by use of temperature averages computed from a nonlinear Q_{10} relationship (Larcher 1975). Thus, we expect production to be better correlated with the product of growing season days x temperature than with growing season days alone. In fact, whether we use our average growing season temperature or growing season Q index, the relationship is poorer for both harvestable ($r^2 = 0.44$) and total ($r^2 = 0.12$) production. Since the basic physiological response is a physiochemical necessity, I deduce first that, while the vegetation of each environmental zone does respond to temperature, it is specifically adapted to temperatures in that zone and, second, that temperature adaptation distinct to each zone eliminates temperature from the predictive equation. I doubt that temperature would be eliminated if adaptation were eliminated by using a genetically homogeneous vegetation type; for example, if the region were vegetated with a single crop, production would be best predicted by the product of growing season length and temperature. Since competitiveness of a tree undoubtedly depends on its productivity relative to competitors, this conclusion supports earlier speculation that growing season temperature adaptation provides at least one basis for the existence of different vegetation zones.

While I have argued that production in a zone is best predicted from the length of its warm moist growing season, I expect the standing crop of mature accumulative (woody) vegetation (table 2) to be largely determined by site fertility. Accumulation—slow or fast—depends on photosynthesis minus respiration. Synthesis depends on

light, warmth, water (open stomates), and nutrients. In the absence of stand destruction, annual inputs of light, warmth, water, and elements with atmospheric cycles (for example, C, H, O, N) should support eternal accumulation. Limited supplies of nutrients with geologic cycles (for example, P, K, Ca) will halt accumulation (Weaver 1978). It is also argued (Odum 1969) that accumulation is halted when respiration equals production. Thus, in young trees net production is high because the ratio of photosynthetic mass to respiratory mass is high, in longer stemmed trees efficiency declines as the respiratory load increases, and growth ceases when respiration equals gross production; heartwood's contribution to this relationship is in proportion to its inertness. While the respiratory factor undoubtedly contributes to observed declines in production with stand height (and age) (Weaver and others 1990), I see nutrient supplies as more limiting in high forests because the trees are far shorter (and therefore more efficient) than productive trees of lower altitudes. In contrast, standing crops in less accumulative (herbaceous) vegetation are determined by production occurring in one growing season, and while it could be determined by supplies of a geologically cycling nutrient, standing crop is more likely determined by a bulk resource like light (unlikely), warmth, water, or an atmospheric nutrient like nitrogen.

CONCLUSIONS

Whitebark pine vegetation is likely excluded from the alpine zone by cool growing season temperatures or droughts occurring most likely in winter. It seems unlikely that freezes of late fall, midwinter, or early spring exclude the tree from higher sites.

The lower physiological limit of whitebark pine is likely set by drought. Its lower realized limit is likely due to competition with lodgepole pine or subalpine fir. By control of competition, managers could probably extend whitebark's range downslope.

The distribution of other dominant plants on the temperature water gradient may be similarly controlled.

Annual production is strongly related ($r^2 = 0.86$) to the number of growing season days. The lack of correlation with temperature suggests that plants of any vegetation zone are adapted to temperature conditions peculiar to that zone. Mature standing crops of woody vegetation are more likely determined by nonatmospheric nutrients than temperature and precipitation. Potential standing crops of herbaceous vegetation, on the other hand, are more likely limited by bulk resources such as warmth, water, carbon, or nitrogen.

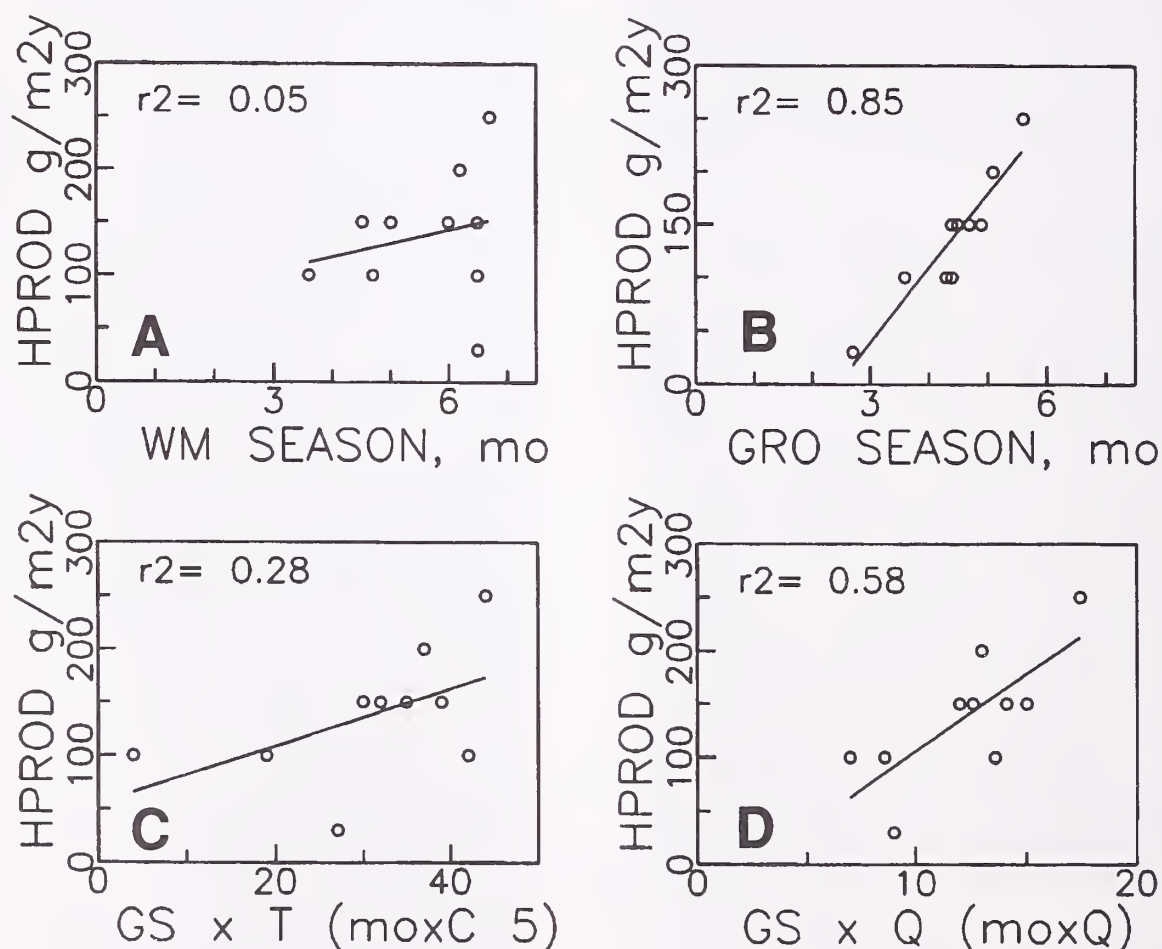


Figure 7—The relationship of harvestable production (HPROD, g/m²/yr) to season length and temperature: (A) production vs. warm season (WM-SEASON), (B) production vs. warm-moist season (GRO-SEASON), (C) production vs. warm-moist season (GS) x average summer temperature above 5 °C (C-5), (D) production vs. warm moist season (GS) x growth support units (Q_{gs}). The ecosystem types are as in figure 1.

ACKNOWLEDGMENTS

I thank colleagues who helped me locate weather stations representative of major environmental types of the region (S. Arno, D. Despain, J. Habeck, R. Rankin, and others acknowledged in Weaver 1980 and 1990), acquire the data (J. Caprio), and choose parameters for study (J. Pickett and J. Brown). The critical review of P. Burgeron, D. Despain, S. Harvey, W. Moir, and D. Perry is greatly appreciated. I am also grateful for the support provided by Intermountain Research Station, USDA Forest Service (INT-92720-RJVA).

REFERENCES

- Aplet, G.; Smith, F.; Laven, R. 1989. Stemwood biomass and production during spruce-fir stand development. *Journal of Ecology*. 77: 70-77.
- Armand, A. 1992. Sharp and gradual mountain timberlines as a result of species interaction. In: Hansen, A.; DiCasteri, F. 1992. *Landscape boundaries*. New York: Springer Verlag: 360-378.
- Arno, S. 1984. Timberline—mountain and arctic forest frontiers. Seattle: Mountaineers. 304 p.
- Arno, S.; Weaver, T. 1990. Whitebark pine community types and their pattern in the landscape. In: Schmidt, W.; McDonald, K., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 97-105.
- Burke, M.; Gusta, L.; Quamme, H.; Weiser, C.; Li, P. 1976. Freezing injury in plants. *Annual Review of Plant Physiology*. 27: 507-528.
- Chang, J. 1968. *Climate and agriculture*. Chicago: Aldine. 304 p.
- Collins, D.; Weaver, T. 1978. Effects of summer weather modification (irrigation in *Festuca idahoensis*-*Agropyron spicatum* grasslands. *Journal of Range Management*. 31: 264-269.
- Daubenmire, R. 1943. Vegetation zonation in the Rocky Mountains. *Botanical Review*. 9: 325-393.
- Daubenmire, R. 1956. Climate as a determinant of vegetation distribution in eastern Washington and northern Idaho. *Ecological Monographs*. 26: 131-154.
- Daubenmire, R. 1970. Steppe vegetation of Washington. *Bull.* 62. Pullman, WA: Washington Agricultural Experiment Station. 131 p.
- Daubenmire, R. 1981. Subalpine parks associated with snow transfer in the mountains of northern Idaho and eastern Washington. *Northwest Science*. 55: 124-135.
- Daubenmire, R.; Daubenmire, J. 1968. Forest vegetation of eastern Washington and northern Idaho. *Bull.* 60. Pullman, WA: Washington Agricultural Experiment Station. 104 p.
- Forcella, F.; Weaver, T. 1977. Biomass and productivity of the subalpine *Pinus albicaulis*/*Vaccinium scoparium* association, MT USA. *Vegetatio*. 35: 95-105.
- Gams, H. 1931. Die klimatische Begrenzung von Pflanzen arealen und die Verteilung der hygrischen Kontinentalitat in den Alpen. *Zeitschrift der Gesellschaft für Erdkunde*. 9: 32-68.
- Gates, D.; Papian, L. 1971. *Atlas of energy budgets of plant leaves*. London and New York: Academic Press. 277 p.
- Geiger, R. 1965. *The climate near the ground*. Cambridge, MA: Harvard University Press. 611 p.
- Hadley, J.; Smith, W. 1987. Influence of krummholz microclimate on needle physiology and survival. *Oecologia*. 73: 82-90.
- Hanley, D. 1976. Tree biomass and production estimates for three habitat types in northern Idaho. *Bull.* 14. Moscow, ID: University of Idaho, College of Forestry. 16 p.
- Hunt, W.; Ingham, E.; Coleman, D.; Elliott, E.; Reid, P. 1988. Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology*. 69: 1009-1016.
- Holdridge, L. 1967. Determination of world plant formations from simple climatic data. *Science*. 130: 572.
- Huschle, G.; Hironaka, M. 1980. Classification and ordination of seral plant communities. *Journal of Range Management*. 33: 179-182.
- Hutchinson, G. 1958. Concluding remarks. *Cold Springs Harbor Symposium in Quantitative Biology*. 22: 415-427.
- Jacobs, J.; Weaver, T. 1990. Effect of temperature and temperature preconditioning on seedling performance of whitebark pine. In: Schmidt, W.; McDonald, K., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 134-139.
- Kuchler, A. 1964. Potential vegetation of the conterminous US. *Spec. Publ.* 36. New York: American Geographical Society. 155 p.
- Landis, T.; Mogren, E. 1975. Tree strata biomass of subalpine spruce-fir stands in SW Colorado. *Forest Science*. 21: 9-12.
- Lanner, R. 1980. Biology, taxonomy, evolution, and geography of the stone pines of the world. In: Schmidt, W.; McDonald, K., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.
- Larcher, W. 1975. *Physiological plant ecology*. New York: Springer. 252 p.
- Neilson, R. 1986. High resolution climatic analysis and southwest biogeography. *Science*. 232: 27-33.
- Nielson, R. 1992. Toward a rule based biome model. *Landscape Ecology*. 7: 27-43.
- Nobel, P. 1983. *Biophysical plant physiology*. San Francisco: Freeman. 608 p.
- Penman, H. 1949. The dependence of transpiration on weather and soil conditions. *Journal of Soil Science*. 1: 74-89.
- Pfister, R.; Kovalchik, B.; Arno, S.; Presby, R. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

- Rodin, L.; Bazilevich, N. 1967. Production and mineral cycling in terrestrial vegetation. London: Oliver and Boyd. 288 p.
- Salisbury, F.; Ross, C. 1992. Plant physiology. Belmont, CA: Wadsworth. 682 p.
- Scott, D.; Billings, W. 1964. Effects of environmental factors on standing crop and production of an alpine tundra. *Ecological Monographs*. 34: 243-270.
- Stephenson, N. 1990. Climatic control of vegetation distribution: the role of water balance. *American Naturalist*. 135: 649-670.
- Thilenius, J.; Smith, D.; Brown, G. 1974. Effect of 2,4-D on composition and production of an alpine plant community in Wyoming. *Journal of Range Management*. 27: 140-142.
- Thorntwaite, C. 1948. An approach toward a rational classification of climate. *Geographical Review*. 38: 55-94.
- Tomback, D.; Hoffmann, L.; Sund, S. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Schmidt, W.; McDonald, K., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-129.
- Tranquillini, W. 1979. Physiological ecology of the alpine timberline. Tree existence at high altitude with special reference to the European Alps. New York: Springer. 137 p.
- U.S. FPL. 1974. Wood handbook: wood as an engineering material. Agric. Handb. 72. Washington, DC: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. [n.p.].
- USGS. 1970. The national atlas. Washington, DC: U.S. Department of the Interior, Geological Survey. 417 p.
- Walter, H. 1973. Vegetation of the earth in relation to climate and ecophysiological conditions. New York: Springer. 237 p.
- Weaver, T. 1978. Changes in soils along a vegetation-altitudinal gradient of the Northern Rocky Mountains. In: Youngberg, C., ed. *Forest soils and land use*. Proceedings; 5th North American Soils Conference. Fort Collins, CO: Colorado State University, Forestry Department: 14-29.
- Weaver, T. 1980. Climates of vegetation types of the northern Rocky Mountains and adjacent plains. *American Midland Naturalist*. 103: 392-398.
- Weaver, T. 1983. Yield response of high plains grasslands to water enrichment, three phases. In: Holman, L.; Knutsen, G. *State of Montana activities in the High Plains Cooperative Program 1981-1983*. Helena, MT: Montana Department of Natural Resources, Water Resources Division: 77-94.
- Weaver, T. 1990. Climates of subalpine pine woodlands. In: Schmidt, W.; McDonald, K., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 72-79.
- Weaver, T.; Collins, D. 1977. Effects of weather modification (increased snow pack) on *Festuca idahoensis* meadows. *Journal of Range Management*. 30: 451-456.
- Weaver, T.; Dale, D. 1974. *Pinus albicaulis* in central Montana: environment, vegetation, and production. *American Midland Naturalist*. 92: 222-229.
- Weaver, T.; Forcella, F. 1977. Biomass of fifty conifer forests and nutrient exports associated with their harvest. *Great Basin Naturalist*. 37: 395-401.
- Weaver, T.; Forcella, F.; Dale, D. 1990. Stand development in whitebark pine woodlands. In: Schmidt, W.; McDonald, K., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 151-155.
- West, N. 1983. Temperate deserts and semideserts: Intermountain salt desert shrubland. Amsterdam: Elsevier: 382.
- Whittaker, R. 1975. Communities and ecosystems. New York: Macmillan. 385 p.
- Whittaker, R.; Niering, W. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. *Ecology*. 56: 771-790.
- Willms, W.; Smoliak, S.; Bailey, A. 1986. Herbage production following litter removal on Alberta native grasslands. *Journal of Range Management*. 39: 536-540.

Regeneration



International Workshop
St. Moritz 1992

VARIATION IN SIZE AND WEIGHT OF CONES AND SEEDS IN FOUR NATURAL POPULATIONS OF CARPATHIAN STONE PINE

I. Blada
N. Popescu

Abstract—High variation was found within populations of stone pine (*Pinus cembra* L.) for seeds per cone and seeds per cone weight, but middle high for 1,000-seed weight and low for cone length and cone diameter. The cone length, cone diameter, seeds per cone, seeds per cone weight, and 1,000-seed weight means were 4.7 cm, 4.2 cm, 37.8 cm, 9.2 g, and 250 g, respectively. Southern populations were similar in cone length and cone diameter, but not in seeds per cone, seeds per cone weight, and 1,000-seed weight. Cone length and cone diameter from open-pollinated, cross-pollinated and self-pollinated cones were similar, while seeds per cone, seeds per cone weight, and 1,000-seed weight, were not. All traits displayed continuous variation. Significant correlations were found among all traits, except 1,000-seed weight.

Stone pine (*Pinus cembra* L.) is naturally distributed in the highest forest zone of the Alps and Carpathian Mountains (Critchfield and Little 1966; Holzer 1975). In the Alps, the low-elevation stands range between 1,100 to 1,500 m, but the main zone extends between 1,700 to 2,000 m (Contini and Lavarello 1982; Holzer 1975), while the high-elevation form of the species climbs as single trees up to 2,700 m above sea level (Moser 1960). In Romania, stone pine ranges from 1,350 to 1,880 m in the northern Carpathians (Gubesch 1971) and from 1,350 to 1,980 m in the southern Carpathians (Beldie 1941; Oarcea 1966; Tataranu and Costea 1952).

Because of its tolerance for low temperatures, the species is very important for reforestation of the subalpine zone; in this zone it is also important on watersheds, for stabilizing avalanche areas, and for reducing the effects of flash floods (Holzer 1972).

Stone pine has a particular importance for the silviculture of the subalpine zone of the Carpathians. For this reason a genetic improvement program with both intra- and interspecific crosses is being carried out (Blada 1982, 1990a); some results have been published (Blada 1987, 1990b, 1992a) or are in preparation (Blada 1992b).

This paper reports on the phenotypic variation in size and weight of cones and seeds in four natural populations of Carpathian stone pine, as part of the program.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

I. Blada and N. Popescu are Forest Geneticists, Forest Research Institute, Bucharest 11, Romania.

MATERIALS AND METHODS

Twenty trees were sampled at random in each of the four populations listed in table 1. In mid-July 1991, 25 cones from open pollination (OP) on each of the 20 trees (total 80 trees) were protected against the mountain jay (*Nucifraga caryocatactes* L.) by using metal net bags 25 by 20 cm in size.

For comparative reasons, cones and seeds obtained from controlled cross- and self-pollinations (CP, SP) in the Gemelele population were measured; these pollinations were performed in July 1989 using 10 x 10 full diallel mating design (Blada 1992b), according to Griffing's (1956) Experimental Method 1.

Cone and seed measurements were taken soon after their collection in October 1990 for controlled cross-pollinated and self-pollinated and in October 1991 for open-pollinated cones. Twenty-five cones were measured from each tree resulting from open-pollinated cones, and 20 cones from each combination resulting from controlled cross-pollinated and self-pollinated cones. Five traits were measured as shown in table 2.

Using data from measurements, the population mean (\bar{x}), standard deviation (σ), mean square (σ^2), variation coefficient (VC), range of variation (Q), and correlation coefficient (r) were calculated.

WITHIN-POPULATION VARIATION

Statistical parameters of the cones and seeds of the four Carpathian stone pine populations listed in table 1 are summarized in table 3 and figure 1.

Table 1—Geographic distribution of *Pinus cembra* studied populations in the Carpathians

Population	Latitude N.	Longitude E.	Altitude	Carpathian Range
	----- Degrees -----		Meters	
Gemelele	45°35'	22°50'	1,720	Southern
Stâna de Râu	45°25'	23°03'	1,450	Southern
Pietrele	45°23'	22°52'	1,550	Southern
Lala	47°33'	25°05'	1,520	Northern

Table 2—Measured traits

Trait	Units	Symbols
Cone length	Centimeters	CL
Cone diameter	Centimeters	CD
Seeds per cone	Number	SC
Seeds per cone weight	Grams	SCW
1,000-seed weight	Grams	1,000-SW

The following main results were obtained for the Gemenele, Stâna de Râu, Pietrele, and Lala populations (in sequence):

- The cone length mean was 4.9 ± 0.4 cm, 4.7 ± 0.4 cm, 4.9 ± 0.6 cm, and 4.1 ± 0.4 cm, respectively.
- The cone diameter mean was 4.2 ± 0.3 cm, 4.1 ± 0.3 cm, 4.1 ± 0.3 cm, and 3.5 ± 0.2 cm, respectively.
- The seeds per cone mean was 40.9 ± 9.6 , 36.7 ± 8.1 , 52.6 ± 13.3 , and 21.1 ± 7.1 , respectively.
- The seeds per cone weight was 9.8 ± 2.7 g, 9.0 ± 2.5 g, 12.5 ± 3.9 g, and 5.6 ± 1.7 g, respectively.

Table 3—Mean (\bar{x}), phenotypic standard deviation (σ), mean square (σ^2), variation coefficient (VC), range of variation (Q)

Trait	Parameters (open pollination)			
	$\bar{x} \pm \sigma$	σ^2	VC	Q
Gemenele population				
CL	4.9 ± 0.4	0.15	7.9	4.1 - 5.8
CD	4.2 ± 0.3	0.11	7.9	3.6 - 5.0
SC	40.9 ± 9.6	91.31	23.3	22.5 - 60.2
SCW	9.8 ± 2.7	7.50	28.0	4.6 - 18.1
1,000-SW	238.0 ± 47.4	2,243	19.9	170 - 352
Stâna de Râu population				
CL	4.7 ± 0.4	0.18	9.1	3.8 - 5.6
CD	4.1 ± 0.3	0.08	7.0	3.7 - 4.9
SC	36.7 ± 8.1	65.67	22.1	21.7 - 55.4
SCW	9.0 ± 2.5	6.05	27.3	5.5 - 14.1
1,000-SW	252 ± 37.6	1,412	14.9	175 - 293
Pietrele population				
CL	4.9 ± 0.6	0.34	11.7	4.1 - 6.0
CD	4.1 ± 0.3	0.10	7.7	3.4 - 4.7
SC	52.6 ± 13.3	177.31	25.3	31.2 - 90.4
SCW	12.5 ± 3.9	15.27	31.3	6.2 - 23.1
1,000-SW	238 ± 60.9	3,712	25.6	138 - 428
Lala population				
CL	4.1 ± 0.4	0.17	9.9	3.7 - 5.1
CD	3.5 ± 0.2	0.04	6.0	3.1 - 3.9
SC	21.1 ± 7.1	51.15	34.0	13.6 - 34.8
SCW	5.6 ± 1.7	2.78	29.9	3.6 - 9.4
1,000-SW	270 ± 46.5	2,163	17.2	184 - 346
Trait parameters across four populations				
CL	4.7 ± 0.5	0.30	11.7	3.7 - 6.0
CD	4.2 ± 0.3	0.11	7.9	3.1 - 5.0
SC	37.8 ± 14.9	222.22	39.4	13.6 - 90.4
SCW	9.2 ± 3.7	13.77	40.3	3.6 - 23.1
1,000-SW	250 ± 49.7	2,471.00	19.8	167.0 - 354.0

- The 1,000-seed weight mean was 238 ± 47.4 g, 252 ± 37.6 g, 238 ± 60.9 g, and 270 ± 46.5 g, respectively.

Therefore, the southern populations were similar in cone length and cone diameter, but not in seeds per cone, seeds per cone weight, and 1,000-seed weight. On the other hand, the southern populations ranked high and the northern population ranked low for all measured traits.

Very high variation coefficients were found within each population for both seeds per cone and seeds per cone weight, but middle high for 1,000-seed weight and low for cone length and cone diameter traits.

The last three columns of table 3 give information concerning mean squares, variation coefficients, and the range of variation for population traits.

ACROSS-POPULATION PARAMETERS

The mean values and ranges of the traits across four studied populations—and by extrapolation—for all the Carpathian stone pine were as follows (table 3, lower part):

- The cone length mean ranged from 3.7 to 6.0 cm, with a mean of 4.7 ± 0.5 cm, and the cone diameter ranged from 3.1 to 5.0 cm, with a mean of 4.2 ± 0.3 cm. According to Contini and Lavarello (1992), the size of cones from the Alps ranged from 5.0 to 10.0 cm in length and from 4.0 to 6.0 cm in diameter. Therefore, the cone size from the Alps ranked high and the cones from the Carpathians ranked low.

- The seeds per cone ranged from 13.6 to 90.4, with a mean of 37.8 ± 14.9 . However, the seeds per cone mean from the Alps varied between 46 and 164 with a mean of 93 seeds (Rohmeder and Rohmeder 1955). Thus, the seeds per cone from the Alps ranked high and the seeds per cone from the Carpathians ranked low.

- The seeds per cone weight mean ranged from 3.6 to 23.1 g, with a mean of 9.2 ± 3.7 g.

- The 1,000-seed weight mean ranged from 167 to 354 g, with a mean of 250 ± 49.7 g. Consequently, a kilogram of seed from the Carpathians could include from 2,825 to 5,988 seeds, with a mean of 4,000 seeds. According to Rohmeder and Rohmeder (1955), the 1,000-seed weight mean from the Alps ranged between 150 and 350 g; thus, the Carpathians 1,000-seed weight mean was very close to that of the Alps.

The cone length, cone diameter, seeds per cone, seeds per cone weight, and 1,000-seed weight coefficients accounted for 11.7 percent, 7.9 percent, 39.4 percent, 40.3 percent, and 19.8 percent of the variation, respectively (table 3, lower part).

POLLINATION COMPARISONS

The cone and seed parameters shown in table 4 came from records of 2,000 cones from 80 open-pollinated (OP) trees, 1,800 cones from a 10 x 10 full diallel mating design for cross-pollination (CP), and 200 cones from 10 self-pollinated (SP) trees, all from the Gemenele population. For example, the cone length ranged from:

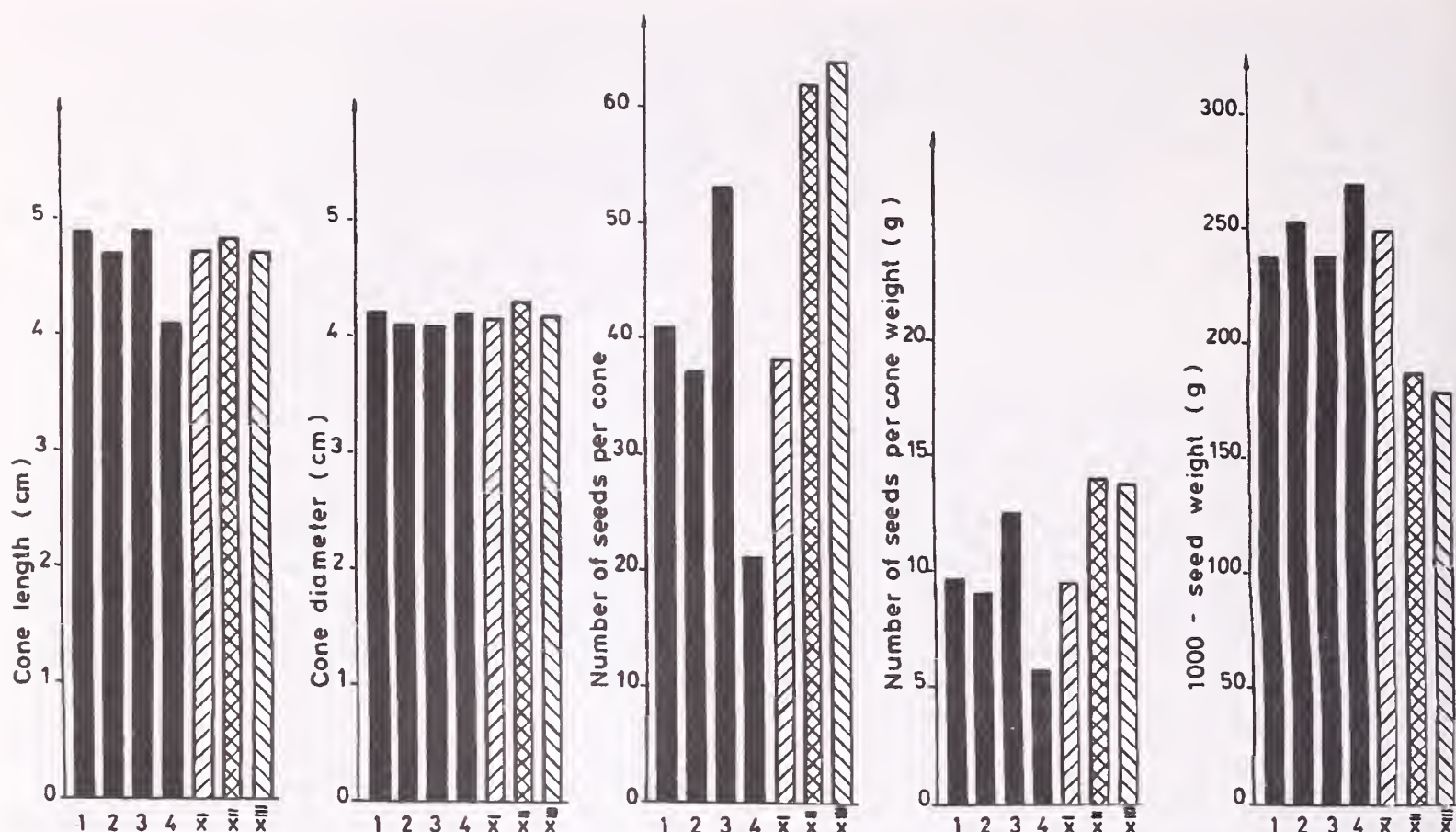


Figure 1—Mean performance of five measured traits of cones and seeds from open pollination in four populations (1, 2, 3, 4) compared to controlled cross-pollination (\bar{x}) and self-pollination (\bar{x}) (\bar{x} = average across 1, 2, 3, 4 populations).

4.1 to 5.8 cm, with a mean of 4.9 ± 0.4 cm for open-pollinated;

3.5 to 6.0 cm, with a mean of 4.8 ± 0.6 cm for cross-pollinated;

3.7 to 5.5 cm, with a mean of 4.7 ± 0.6 cm for self-pollinated.

Variation coefficients (VC) for open-pollinated, cross-pollinated, and self-pollinated were 7.9 percent, 12.8 percent, and 12.1 percent, respectively.

Table 4—Comparison between statistical parameters of cones and seeds in the Gemelele population, according to the pollination type

Trait	Type of pollination ¹	Parameters			
		$\bar{x} \pm \sigma$	σ^2	VC	Q
CL	OP	4.9 \pm 0.4	0.15	7.9	4.1 - 5.8
	CP	4.8 \pm 0.6	0.37	12.8	3.5 - 6.0
	SP	4.7 \pm 0.6	0.36	12.1	3.7 - 5.5
CD	OP	4.2 \pm 0.3	0.11	7.9	3.6 - 5.0
	CP	4.3 \pm 0.4	0.15	9.1	3.7 - 5.4
	SP	4.2 \pm 0.4	0.16	9.4	3.6 - 4.9
SC	OP	40.9 \pm 9.6	91.31	23.3	22.5 - 60.2
	CP	62.0 \pm 16.5	272.24	26.6	41.4 - 96.4
	SP	64.0 \pm 12.9	167.12	20.3	44.9 - 85.7
SCW	OP	9.8 \pm 2.7	7.50	28.0	4.6 - 18.1
	CP	14.1 \pm 4.4	19.56	31.3	7.0 - 24.5
	SP	13.8 \pm 3.1	9.66	22.5	9.5 - 17.6
1,000-SW	OP	238.0 \pm 47.4	2,243.00	19.9	170.0 - 352.0
	CP	188.0 \pm 31.3	978.00	16.6	11.7 - 26.5
	SP	179.0 \pm 25.6	656.94	14.3	14.7 - 22.3

¹OP = open pollination; CP = controlled cross-pollination in a 10 x 10 diallel; SP = self pollination of 10 parents.

Similar data can be found for cone diameter, seeds per cone, seeds per cone weight, and 1,000-seed weight in table 4.

CORRELATIONS

Significant ($p < 0.05$) and highly significant ($p < 0.01$) correlations were found between cone length and cone diameter, cone length and seeds per cone, cone length and seeds per cone weight; cone diameter and seeds per cone, cone diameter and seeds per cone weight; seeds per cone and seeds per cone weight. No significant correlation was found between 1,000-seed weight and any other trait (table 5). These strong correlations among the main cone and seed traits suggest that improvement (quantitatively) of seed production could be made by indirect selection; for example, selection for cone length, as an easily measurable trait, will cause an increase in seeds per cone and seeds per cone weight, and consequently in seed production.

TYPE OF DISTRIBUTION

The distribution frequencies of cone length, cone diameter, seeds per cone, seeds per cone weight, and 1,000-seed weight were very close to normal distribution (fig. 2). According to genetic theory (Mather and Jinks 1977), this pattern of distribution is specific to quantitative traits. Such traits are polygenically controlled.

Table 5—Phenotypic correlations among *Pinus cembra* cone and seed traits (Df = 18)

Trait	CL	CD	SC	SCW	1,000-SW
CL	1.000	0.577**	0.636**	0.669**	0.272
CD		1.000	0.499*	0.647**	0.227
SC			1.000	0.636**	0.325
SCW				1.000	0.396
1,000-SW					1.000

DISCUSSION

Our observations in the main Carpathian populations indicated that tree, locality, and year in which the cones were initiated may significantly affect cone and seed traits. As the measurements were performed on cones collected in two different years, the comparisons were perhaps not entirely valid.

The seeds per cone and seeds per cone weight from open-pollinated cones ranked lower than the same parameters from both cross-pollinated and self-pollinated cones; but, surprisingly, 1,000-seed weight from open-pollinated cones ranked higher than 1,000-seed weight from cross-pollinated cones. The lack of significant correlation between 1,000-seed weight and seeds per cone weight (table 5) partially explains this unexpected result. Also, these differences could be attributable to the biological and climatic factors (temperature, moisture, and wind) that occurred in 1990 and 1991.

The cone length and cone diameter means from self-pollinated cones were similar to cone length and cone diameter means from both open-pollinated and cross-pollinated cones, but the seeds per cone and seeds per cone weight means from self-pollinated cones were similar to seeds per cone and seeds per cone weight means from cross-pollinated cones and ranked higher than open-pollinated cones. Consequently, stone pine was found

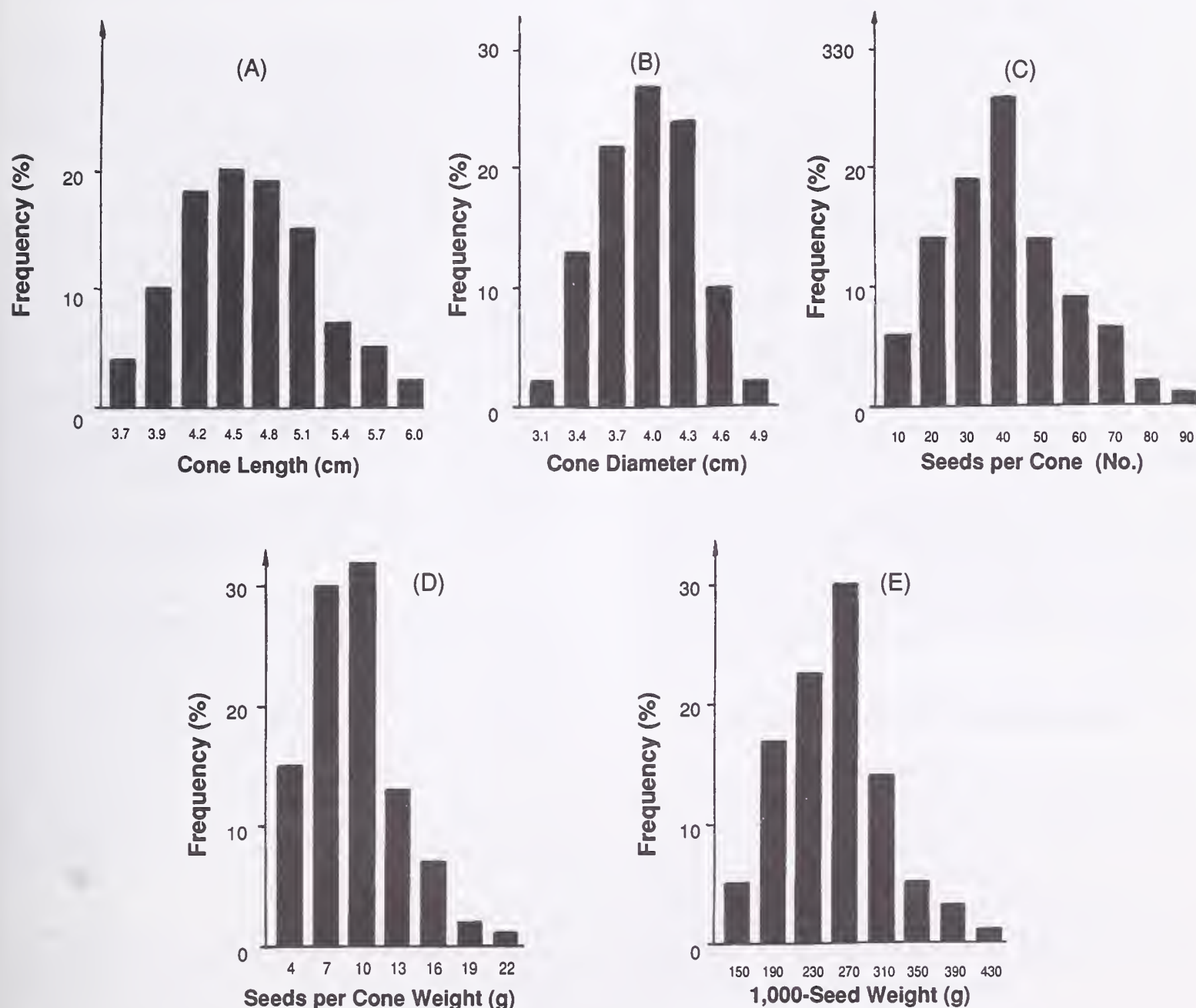


Figure 2—Frequency distribution in the *Pinus cembra* populations evaluated for five traits.

to be highly self-fertile. This led to the conclusion that a very high proportion of the seeds produced by wind pollination would be selfs; this is an undesirable characteristic since selfed seed produces slower growing trees and the seedlings have a lower survival rate.

Finally, it should be stressed that although the stone pine cone diameter, cone length, and seeds per cone means from the Alps exceeded the same trait means from the Carpathians, the 1,000-cone weight mean from the Carpathians was similar to that from the Alps.

CONCLUSIONS

Southern populations were similar in cone length and cone diameter but not in seeds per cone, seeds per cone weight, and 1,000-seed weight. Southern populations ranked high and the northern ones ranked low in all measured traits.

Very high variation in both seeds per cone and seeds per cone weight was found within each population, but variation in 1,000-seed weight was moderate, and it was low in cone length and cone diameter traits.

Cone length and cone diameter from open-pollinated, cross-pollinated, and self-pollinated cones were similar, while seeds per cone, seeds per cone weight, and 1,000-seed weight were not.

The strong correlations among the main cone and seed traits suggest that genetic improvement in seed production could be attained by indirect selection.

All measured traits displayed a continuous variation, suggesting polygenic control.

ACKNOWLEDGMENTS

Gratitude is expressed to Dr. H. Kriebel from Ohio State University for the revision of the English version of the paper and for the useful suggestions.

REFERENCES

- Beldie, A. 1941. Observatii asupra vegetatiei lemnoase din Muntii Bucegi. *Analele ICEF*, Seria I, vol. 6: 39-43.
- Blada, I. 1982. Relative blister rust resistance of native and introduced white pines in Romania. In: Heybroek, H.; [and others], eds. *Resistance to diseases and pests in forest trees*. PUDOC, Wageningen, The Netherlands: 415-416.
- Blada, I. 1987. Genetic resistance to *Cronartium ribicola* and height growth in some five needle pines and of some inter-specific hybrids. Bucharest: Academy of Agricultural and Forestry Sciences. 146 p. Thesis.
- Blada, I. 1990a. Breeding *Pinus cembra* by intra- and inter-specific crosses. For. Res. Inst., Bucharest, Research Plan, No. 7/1990.
- Blada, I. 1990b. Genetic variability of some traits in two *Pinus cembra* natural populations. In: Garrett, P. W., ed. *Proceedings of a symposium on white pines provenances and breeding*. Gen. Tech. Rep. NE-155. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 56-68.
- Blada, I. 1992a. *Pinus cembra* and its inter-specific hybrids. Paper presented at the IUFRO Centennial Meeting, Berlin-Eberswalde, August 31-September 5, 1992.
- Blada, I. 1992b. Diallel cross in *Pinus cembra*. I. Variation in cone and seed traits. [In preparation].
- Contini, L.; Lavarelo, Y. 1982. *Le pin cembro: repartition, ecologie, sylviculture et production*. Paris: INRA, ISBN. 197 p.
- Critchfield, W. B.; Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Australian J. Sci.* 9: 465-493.
- Gubesch, L. 1971. Raspadirea relictului glaciar zambrul (*Pinus cembra*) pe versantii sudici ai unor masive din Calimani. *Ocotirea Naturii*, 15, 2: 149-159.
- Holzer, K. 1972. Intrinsic qualities and growth potential of *Pinus cembra* and *P. peuce* in Europe. In: Bingham, R. T.; [and others], eds. *Biology of rust resistance in forest trees*. Misc. Publ. Washington, DC: U.S. Department of Agriculture, Forest Service: 99-110.
- Holzer, K. 1975. Genetics of *Pinus cembra* L. *Anales Forestales, Zagreb*. 6/5: 139-158.
- Mather, K.; Jinks, J. L. 1977. *Introduction to biometrical genetics*. Chapman and Hall, Ltd. 233 p.
- Moser, L. 1960. Verbreitung und Bedeutung der Zirbe im italienischen Alpengebiet. *Jb. Ver. Z. Schutz Alpenpfl.u.-tiere*. 25: 16-21.
- Oarcea, Z. 1966. Contributii la cunoasterea raspandirii si vegetarii pinului cembra in Retezat. *Revista Pad.* 9: 495-497.
- Rohmeder, E.; Rohmeder, M. 1955. Untersuchungen uber das Samentragen und Keimen der Zirbelkiefer (*Pinus cembra*) in den Bayrischen Alpen. *Allg. Forstzeitschrift*. 10: 83.
- Tataranu, I. D.; Costea C. 1952. Un arbore de interes forestier: *Pinus cembra*. *Revista Padurilor*. 11: 3-14.

ROLE OF NUTCRACKERS ON SEED DISPERSAL AND ESTABLISHMENT OF *PINUS PUMILA* AND *P. PENTAPHYLLA*

Mitsuhiro Hayashida

Abstract—Nutcrackers (*Nucifraga caryocatactes*) harvest almost all *Pinus pumila* Regel cones and cache the seeds in the soil. Most *P. pentaphylla* Mayr seeds scatter after the cones open, while nutcrackers collect the seeds still held in the cones and then cache the seeds. Many seedlings of *P. pumila* and *P. pentaphylla* are often found in clusters consisting of several individuals of the same age. Almost all *P. pumila* seedlings and clusters of *P. pentaphylla* seedlings on barren slopes likely originate from seeds cached by nutcrackers.

Stone pines (subsection *Cembrae* in *Pinus*) have large wingless seeds that are dispersed by caching of vertebrates (Hayashida 1989a; Hutchins and Lanner 1982; Mattes 1982; Tomback 1982). Nutcrackers (*Nucifraga* spp.) are the main dispersal agents of seeds of these pines (Lanner 1989). The nutcracker also caches other large wingless seeds or short-winged seeds in section *Strobus* (Lanner and Vander Wall 1980; Tomback 1990; Vander Wall and Balda 1977).

Pinus pumila Regel (Japanese stone pine) is a dwarf pine. Its range extends through Japan and Korea into Siberia, Kamchatka (Critchfield and Little 1966). On most of the high mountains in Japan, a vegetational zone dominated by *P. pumila* occurs above the forest limit. This area is called the "*Pinus pumila* zone" by Japanese ecologists. The regeneration of *P. pumila* thickets is mainly due to a vegetative regeneration by adventitious roots (Okitsu and Ito 1983). Large wingless seeds of *P. pumila* are known to be dispersed by nutcrackers (Saito 1983; Turcek and Kelso 1964), but a detailed observation for seed dispersal and caching behavior is needed.

Pinus parviflora Sieb. et Zucc. (Japanese white pine) is distributed throughout the Japanese islands (Critchfield and Little 1966). This species consists of two geographical varieties, which intergrade in central Japan (Hayashi 1954). The northern variety is sometimes called *P. pentaphylla* Mayr; the southern *P. himekomatsu* Miyabe and Kudo or a variety of the former. Since the seed wings of *P. pentaphylla* are longer than those of *P. himekomatsu* (Ishii 1968), I distinguished between the two pines. There are few ecological studies of these pines except for community structure (Tatewaki and others 1960; Yoshioka and Saito 1962).

Pinus pumila and *P. pentaphylla* are in the subgenus *Strobus* and are so similar that they naturally hybridize (*P. hakkodensis* Makino) (Ishii 1968); but these pines differ in seed, cone, and other characteristics. The objectives of this paper are to describe the processes from seed dispersal to seedling establishment of *P. pumila* and *P. pentaphylla* and to examine the role of nutcrackers in their regeneration.

STUDY AREA

The study was conducted on Mount Apoi (811 m above sea level), which is located in south-central Hokkaido, Japan (42°6' N., 143°2' E.). It is composed of ultramafic rocks (dunite, lherzolite, etc.) (Niida 1984), and is covered with coniferous forests. The *P. pumila* zone extends from elevations of 500 m to 800 m. Below 500 m, *P. pentaphylla* forest occupies the rocky slopes and ridges, while the greater part of the mountain is covered by coniferous forests dominated by *Picea glehnii*, *Pinus pentaphylla*, and *Abies sachalinensis* (Hayashida 1989b).

METHODS

The number and distribution of 2-year cones were mapped to determine rates of seed predation by vertebrates and insects. These cones were counted from July to October in 1984-87. The observations on seed harvesting, transporting, caching, and retrieving behavior in vertebrates were made in 1984-87 using binoculars and a telescope.

Many seedlings of *P. pumila* and *P. pentaphylla* were found on barren slopes along mountain trails. These seedlings were often found in clusters, which consisted of several seedlings of the same age. To obtain the frequency distribution of number of individuals per cluster in both pines, all seedlings on barren slopes along mountain trails were recorded.

SEED AND CONE MORPHOLOGY

Pinus pumila has wingless seeds; *P. pentaphylla* seeds have wings that are seed length (table 1). Seeds of both pines have the same thick coats. *Pinus pumila* seeds are significantly heavier than those of *P. pentaphylla*, though the seeds of *P. pentaphylla* are larger.

Pinus pumila cones do not open when they ripen, but *P. pentaphylla* cones open at maturity and release seeds to fall free. *Pinus pumila* cones weigh less than *P. pentaphylla* cones, but contain more seeds.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Mitsuhiro Hayashida is Associate Professor, Department of Bioenvironment, Faculty of Agriculture, Yamagata University, Wakaba, Tsuruoka 997, Japan.

Table 1—Seed and cone characteristics of *Pinus pumila* and *P. pentaphylla*

Measurement	<i>Pinus pumila</i>		<i>P. pentaphylla</i>		p ¹
	Mean ± SD	N	Mean ± SD	N	
Seed length (mm)	7.700 ± 0.600	105	10.000 ± 0.700	105	0.001
Dry weight (g)	0.100 ± 0.014	36	0.068 ± 0.014	20	0.001
Seed coat thickness (mm)	0.390 ± 0.040	20	0.390 ± 0.040	20	NS
Length of wings (mm)	wingless		10.500 ± 1.600	105	—
Cone mass (g)	11.000 ± 3.300	32	24.800 ± 7.000	27	0.001
Number of seeds per cone	42.800 ± 12.900	45	28.900 ± 9.100	38	0.001
Dehiscence	not open		open		

¹Mann-Whitney U test.

SEED DISPERSAL OF *P. PUMILA*

Figure 1 shows the seasonal disappearance of 2-year cones of *P. pumila* in 1985-88. All cones disappeared from trees by mid-October every year. I observed nutcrackers (*Nucifraga caryocatactes*), squirrels (*Sciurus vulgaris orientis*), and chipmunks (*Tamias sibiricus lineatus*) harvesting cones. Five species of vertebrates harvested and carried seeds to caches: nutcracker, varied tit (*Parus varius*), nuthatch (*Sitta europaea*), squirrel, and chipmunk. The nutcracker was the most frequently observed vertebrate carrying *P. pumila* seeds.

Nutcrackers usually harvest seeds by removing the cones and flying with them to perches where they extract the seeds and hold them in their sublingual pouches. Varied tits and nuthatches were able to take *P. pumila* seeds exposed by nutcracker foraging and eat them. They were seen caching pine seeds on a tree or in the soil. Squirrels visited the *P. pumila* scrub from a coniferous forest to forage on pine seeds. They often carried a whole cone to cache it in scatter-hoarding. Chipmunks harvest pine seeds in their cheek pouches. They carried about 50 seeds on a trip and cached them in the soil.

These results indicate that nutcracker is the main seed disperser of *P. pumila*.

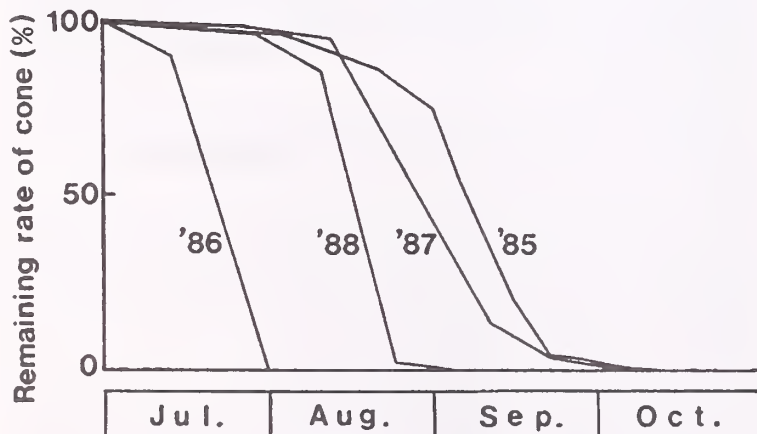


Figure 1—Retention of mature cones of *Pinus pumila* on trees (in years 1985-88) as related to season.

SEED DISPERSAL OF *P. PENTAPHYLLA*

Cones taken by vertebrates or damaged by insects (cone-boring lepidopteran larvae) accounted for less than 20 percent of the total. Usually, nearly 90 percent of the cones open on the trees from mid-September through early October. After opening, about 80 percent of the seeds immediately scatter to the ground, due to the fact that 77 percent of *P. pentaphylla* cones were oriented downward (Hayashida 1989b).

Nutcrackers, varied tits, and nuthatches harvested and cached seeds still held in the upward-oriented open cones. In the years when *P. pumila* crop sizes were small, nutcrackers harvested *P. pentaphylla* seeds more frequently. They extracted the several seeds from an open cone, peeled off the seed wings, and put seeds into their sublingual pouches. They moved rapidly around a tree and went from tree to tree.

NUTCRACKER CACHING BEHAVIOR

Nutcrackers began to cache *P. pumila* seeds in early August when the seeds were mature, and they continued to harvest seeds until the seed crop was depleted. They cached the seeds in the soil at a depth of 2 to 3 cm. Cache size (the number of seeds per cache) ranged from 1 to 51. Nutcrackers cached *P. pumila* seeds mainly in coniferous forests.

In mid-September, *P. pentaphylla* cones began to open, then nutcrackers began to harvest seeds from the opening cones. Nutcrackers scatter-hoarded almost all seeds in the soil (97 percent) except for two caches containing one and two seeds that were established in the bark on fallen trees. Cache size ranged from 1 to 40 seeds. Seventy-eight caches were recorded in coniferous forests and only one cache in the *Pinus pumila* zone.

CLUMPS OF SEEDLINGS

Eighty-four percent of the occurrence of *P. pumila* seedlings were in groups of two or more trees (table 2). These seedlings were 1 km in distance from the nearest seed tree.

Table 2—Number of individuals per clump of *Pinus pumila* and *P. pentaphylla* on barren slopes along mountain trails

Species	Number of clumps (percent)		Number of individuals per clump	
	Single	Clump (2≤)	Maximum	Mean ± SD
<i>Pinus pumila</i>	9 (16)	47 (84)	26	5.6 ± 5.3
<i>P. pentaphylla</i>	137 (72)	54 (28)	25	2.6 ± 3.8

Twenty-eight percent of *P. pentaphylla* seedlings were growing in groups of two or more trees. There were many seed trees of *P. pentaphylla* along the mountain trails. Single seedlings might originate from naturally scattered fallen seeds, and the seedlings in clumps probably originated from caches by nutcrackers.

DISCUSSION

All mature cones of *P. pumila* are harvested by vertebrates every year (fig. 1). My observations indicate that almost all of the transported seeds were carried by nutcrackers. Nutcrackers cached seeds in the soil at a depth of 2 to 3 cm. It is shallow enough to permit seedling establishment. Therefore, seed dispersal of *P. pumila* is heavily dependent on seed caching by nutcrackers.

Nutcrackers carried and cached *P. pumila* seeds mainly into coniferous forests. In general, *P. pumila* seedlings cannot grow and establish in coniferous forests even if cached seeds survive and germinate. However, several *P. pumila* trees were found that developed and matured on the rocky ridges or barren slopes in coniferous forests. These facts may indicate that the nutcracker is not an efficient seed disperser of *P. pumila* under the present conditions. *Pinus pumila* adapted its specialized tree form and other features to the habitat that is characterized by strong winds and heavy snow accumulation in winter. Thus, the *P. pumila* zone is developed on deforested areas in the boreal subalpine belt. In Europe, nutcrackers cached *P. cembra* seeds in coniferous stands and sometimes cached them above timberline (Mattes 1982). Seed dispersal over wide areas by nutcrackers probably played an important role in expanding the range of *P. pumila*.

Pinus pentaphylla has dehiscent cones and winged seeds. Most of the seeds scattered when cones opened. Nutcrackers often harvested and cached seeds still held in the upward open cones. About 90 percent of *P. pentaphylla* trees found in coniferous forests were individual single trees, but on the ecotone between coniferous forest and the *Pinus pumila* zone, half of the occurrences of trees were in clumps of two or more individuals (Hayashida 1989b). About 30 percent of the seedlings were growing in clumps on barren slopes in the coniferous forest zone. These seedlings in clumps probably originated from seeds cached by nutcrackers. Seed dispersal by nutcrackers enables *P. pentaphylla* to invade areas that are inaccessible to other coniferous trees.

The northern variety, *P. pentaphylla*, has longer seed wings than the southern variety, *P. himekomatsu* (Ishii 1968). It is possible that these two varieties have different

morphological features and seed-dispersal syndromes. If so, why? I would study these problems with an ecological approach.

ACKNOWLEDGMENTS

I thank Urakawa Local Forest Management Office, Hokkaido, and Oji Forestry and Landscaping Co. for permission to work in the area and for information on the area.

REFERENCES

- Critchfield, W. B.; Little, E. L., Jr. 1966. Geographic distribution of pine of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Hayashi, Y. 1954. The natural distribution of important trees, indigenous to Japan. Conifers Rep. 3. Bulletin of the Government Forestry Experiment Station. 75: 1-173. [In Japanese with English summary].
- Hayashida, M. 1989a. Seed dispersal by red squirrels and subsequent establishment of Korean pine. Forest Ecology and Management. 28: 115-129.
- Hayashida, M. 1989b. Seed dispersal and regeneration pattern of *Pinus parviflora* var. *pentaphylla* on Mt. Apoi in Hokkaido. Research Bulletins of the College Experiment Forests, Faculty of Agriculture, Hokkaido University. 46(1): 177-190. [In Japanese with English summary].
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia. 55: 192-201.
- Ishii, S. 1968. The basic forestry study on genus *Pinus*, especially its taxonomic and geographical consideration. Journal of the Faculty of Agriculture, Kochi University. 19: 1-114. [In Japanese with English summary].
- Lanner, R. M. 1989. Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.
- Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. Journal of Forestry. 78: 637-639.
- Mattes, H. 1982. Die Lebensgemeinschaft von Tannenhäher, *Nucifraga caryocatactes* (L.), und Arve, *Pinus cembra* L., und ihre forstliche Bedeutung in der oberen Gebirgswaldstufe, Berichte. 241. 74 p.

- Niida, K. 1984. Petrology of the Horoman ultramafic rocks in the Hidaka Metamorphic Belt, Hokkaido, Japan. *Journal of the Faculty of Science, Hokkaido University, Ser. IV.* 21: 197-250.
- Okitsu, S.; Ito, K. 1984. Vegetation dynamics of the Siberian dwarf pine (*Pinus pumila* Regel) in the Taisetsu mountain range Hokkaido, Japan. *Vegetatio.* 58: 105-113.
- Saito, S. 1983. Caching of Japanese stone pine seeds by nutcrackers at the Shiretoko Peninsula, Hokkaido. *Tori.* 32: 13-20. [In Japanese with English summary].
- Tatewaki, M.; Tsujii, T.; Kawano, S. 1960. The community structure and distribution of *Pinus parviflora* forest in Hokkaido. *Japanese Journal of Ecology.* 10: 120-123. [In Japanese with English summary].
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology.* 51: 451-467.
- Tomback, D. F. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology.* 4: 185-219.
- Turcek, F. J.; Kelso, L. 1968. Ecological aspects of food transportation and storage in the Corvidae. *Communications in Behavioral Biography, Al:* 277-297.
- Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs.* 47: 89-111.
- Yoshioka, K.; Saito, K. 1962. Differences in the distribution of forest communities due to topography of the habitats in Okunikkawa, Miyagi Prefecture. *Ecological Review.* 15: 213-220.

ROLE OF VARIOUS ANIMALS IN DISPERSAL AND ESTABLISHMENT OF WHITEBARK PINE IN THE ROCKY MOUNTAINS, U.S.A.

Harry E. Hutchins

Abstract—The dispersal and establishment of whitebark pine has been attributed to Clark's nutcracker. But what is the role of other animals who forage on whitebark pine seed? This study looks at the role of the diurnal birds and mammals that forage on whitebark pine cones and seed in western Wyoming. A total of 1,005 cones were carefully observed in both contiguous "forest" stands and open-grown "meadow" trees in early November. Red squirrels harvested most of the whitebark pine seed in forested plots while Clark's nutcracker removed most of the seed from the meadow trees. Only a small percentage of seed went to ground squirrels, chipmunks, Stellar's jays, ravens, etc. The foraging behavior as well as the importance of these animal species to whitebark pine regeneration is discussed.

Many animal species have been observed foraging on the nutritious seeds of whitebark pine (*Pinus albicaulis*). But exactly which of these animals plays a role in seedling establishment and to what degree? Which animals are seed predators? Can whitebark pine seed germinate from that seed which is dropped through animal foraging accidents? Do animals harvest all the seed in the fall or can cones fall to the ground and seed germinate as the cone decays? This paper will address these questions.

The role of various animals in the dispersal and establishment of whitebark pine was examined by observing 1,005 cones and determining where and how the seeds were dispersed. By primarily observing the behavior of diurnal birds and mammals in the subalpine canopy, I was able to determine the degree of influence each species has on seed dispersal and seedling establishment.

METHODS

The study was primarily conducted at the Squaw Basin-Togwotee Pass area (Bridger-Teton National Forest; fig. 1). This area of high-elevation meadows offered distant views of bird activity, whitebark pine growing in both contiguous forest and open-grown situations, and an abundant cone crop for whitebark pine during 1980. Besides whitebark pine, the forest stands were composed of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and a minor amount of lodgepole pine (*Pinus contorta*). The moraine meadow ridges were pioneered by

lone whitebark pine. This provided an opportunity to study two different types of communities—"forest" and "meadow" (fig. 2).

Observations of animal activity were also made at Mount Washburn (2,680 to 3,140 m, Yellowstone National Park, WY) and Surprise Lake (2,960 m, Grand Teton National Park, WY). These areas were similar to the Squaw Basin site except they lacked open-grown, cone-bearing trees. Details on the study sites can be found in Hutchins and Lanner (1982) and Vander Wall and Hutchins (1983).

Several cone-bearing whitebark pines were chosen for observation in both continuous forest in which red squirrels (*Tamiasciurus hudsonicus*) were present and in the open meadow, at least several hundred meters from the nearest forest edge (these sites lacked squirrels). In each of these two types of sites, 1,005 whitebark pine cones were observed during the period July 3 to November 2, 1980. The cones were scattered among several mature trees and were counted at 1- to 2-week intervals using a 15-25 x 60-mm spotting scope. Counts were made by standing in a specific marked location and "mapping" the cones on clear acetate. Changes in the "cone map" at each observation were recorded, including the partial removal of a cone. Cone count data were converted into seeds using an empirically derived value for the mean number of seeds per cone (50.4 seeds/cone, Hutchins 1982). Partially consumed cones were tallied by estimating from the ground the percentage of seed remaining as described in Hutchins and Lanner (1982). The seed harvest data were then plotted against cumulative time for both forest and meadow sites. At each observation date samples of seeds were collected to determine maturity and condition. The numbers of filled, discolored, insect-attacked, and second-year-aborted ovules were tallied. Mean dry weight of shelled seeds, seed coat thickness, and caloric content of shelled seeds were all obtained. Germination tests were also conducted with seeds collected at 10 collection dates during the 1980 field season.

Seedfall (caused by animal foraging) below the tree was estimated by placing five, 1-m² wire mesh seed traps randomly below trees. The tops of the seed traps were designed to let seed fall through but to exclude rodents. Data on the number of cones in the tree, the area of the tree crown, and the number of seeds falling per square meter were used to estimate the magnitude of seed fall.

Predation on seed caches of whitebark pine was also studied in 1979 and 1980. I simulated three types of caches: (1) seed that lands on the soil surface from foraging accidents; (2) seed cached at a depth of 3 cm

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Harry E. Hutchins is Natural Resource Instructor, Itasca Community College, Grand Rapids, MN.

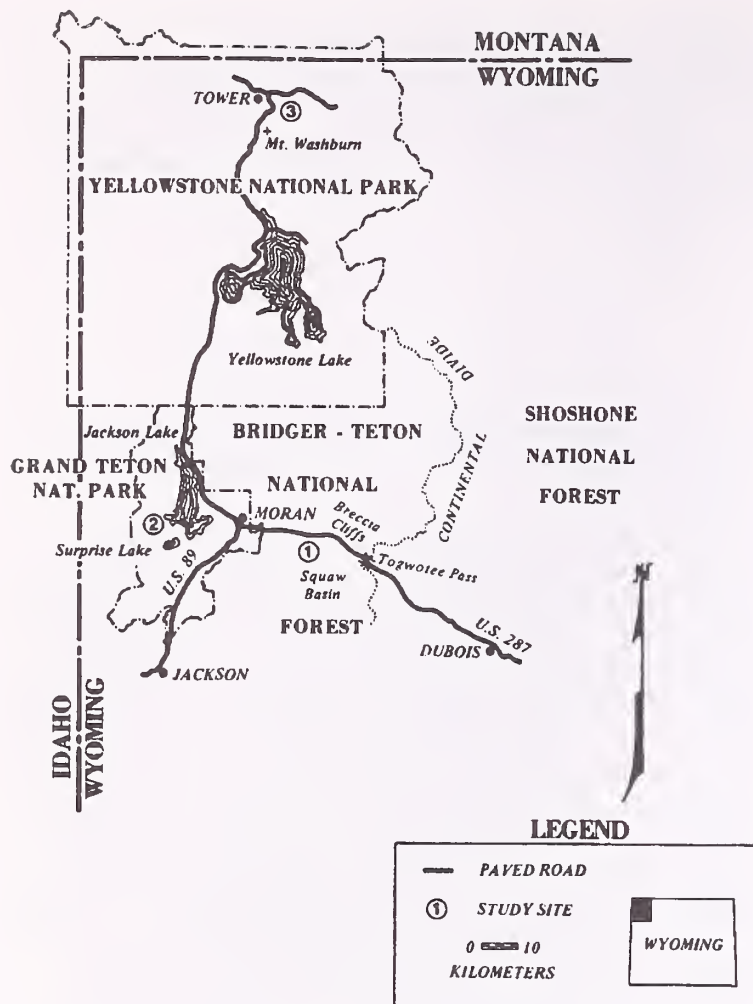


Figure 1—Locations of three study sites in Wyoming.

simulating a Clark's nutcracker (*Nucifraga columbiana*) cache; and (3) seed cached 7 cm deep, which simulates the most shallow red squirrel seed cache. Each individual cache contained 10 seeds.

Animal time budget data were collected for the diurnal species found foraging in the whitebark pine ecosystem. Both quantitative and qualitative observations were made on the various activities and behaviors of the animals; the methods are detailed in Hutchins and Lanner (1982).

SEED DEVELOPMENT

Hutchins and Lanner (1982) monitored seed development and found mean seed coat thickness and seed weight to be significantly greater during the August 31 to November 2 collecting period than prior to these dates. Clark's nutcrackers were unable to extract whole seed from a cone until August 13 due to the thin, fragile seed coats. The characteristic shell fragments of an unripened "nutcracker cone" were left as evidence of their foraging attempts. Thus, nutcrackers were unable to cache whole seed until after this date.

By September 7-10, the cones had dried and turned a dull brown from their previous moist, pitch-filled, purple color. Whitebark pine cones are often referred to as indehiscent; however, about 25 percent of the cones collected after September 7 parted their scales slightly (4-8 mm; $n = 141$). This still was not enough of an opening to allow the seeds to fall out on their own accord.



Figure 2—View of Squaw Basin, WY, showing open-grown whitebark pine in the foreground (meadow plots), forested moraines across the drainage (forest plots), and the Breccia Cliffs in the background.

SEED CROP DEPLETION

Figure 3 (from Hutchins and Lanner 1982) shows seed crop depletion followed a logistic curve ($r^2 = 0.99$ in the forest and $r^2 = 0.96$ in the meadow). Seed harvesting began somewhat earlier in the forest than in the meadow. In fact, about 50 percent of the seed crop had been harvested in the forest by August 31, while in the meadow this point was not attained until September 25. As seen on the graph, no seeds remained from this mast year in the forest stands by November 1. Only 0.1 percent of the seeds still resided in the tree crowns of the meadow trees, and these were no longer there when checked on 27 June, 1981.

Unless aided by an animal, cones of whitebark pine do not fall off a tree to the ground except rarely during extremely large cone crops—as occurred in 1989 (Hutchins and Lanner 1982; Lanner 1982; Mattson and Reinhart, these proceedings). The following incident shows the extent Clark's nutcracker will go to acquire seed. Hutchins and Lanner (1982) placed double-layer wire hardware screening over several cones so there would be cones to collect for germination studies. By late October—after available whitebark pine seeds had become scarce—the nutcrackers had ripped open the screening and harvested the seed. Seed that does drop to the ground from foraging accidents made up only 4.2 percent of the seed crop and most of this seed (69 percent) was determined unviable through examination of the contents in the shell during 1980 (Hutchins 1990).

ANIMAL INTERACTIONS WITH SEED

A variety of diurnal animals were observed active in or under whitebark pine trees. Many of these, however, were never observed foraging on whitebark pine seed in this study. These include: gray jay (*Perisoreus canadensis*),

common flicker (*Colaptes auratus*), Cassin's finch (*Corapodacus cassinii*), rosy finch (*Leucosticte* sp.), pine siskin (*Spinus pinus*), dark-eyed junco (*Junco hyemalis*), black billed magpie (*Pica pica*), pine marten (*Martes americana*), coyote (*Canis latrans*), and weasel (*Mustela* sp.).

Many feces of the mammal species were examined, but no evidence of whitebark pine seeds was found. Gray jays were commonly found in the crowns of whitebark pine but were only observed hawking insects and caching fresh carrion or boli in pine branches. Dow (1965) found this species has little interest in pine seed during feeding trials, although Turcek and Kelso (1968) describe its Eurasian cousin, the European jay (*P. infustus*), as having been observed taking and caching Siberian stone pine (*Pinus sibirica*).

Of the birds, only the magpie could potentially be involved in the dispersal of whitebark pine (Smith and Balda 1979). It is, however, very rare in the subalpine zone during the maturation of whitebark pine seed (Hutchins and Lanner 1982); consequently, any potential harvesting of seed would be unimportant to the regeneration of whitebark pine.

Many species have been observed foraging on whitebark pine cones (Hutchins 1990, table 2). At this point I would like to take a closer look at their role in the dispersal and establishment of this pine.

BIRD DISPERSERS

Clark's Nutcracker—Nutcrackers were the most common resident bird to visit the whitebark pine trees (Hutchins and Lanner 1982). They were scattered about whitebark pine stands in loose flocks foraging and caching seed of this tree. They are dependent on these caches year round (Giuntoli and Mewaldt 1978; Vander Wall and Balda 1977; Vander Wall and Hutchins 1983).

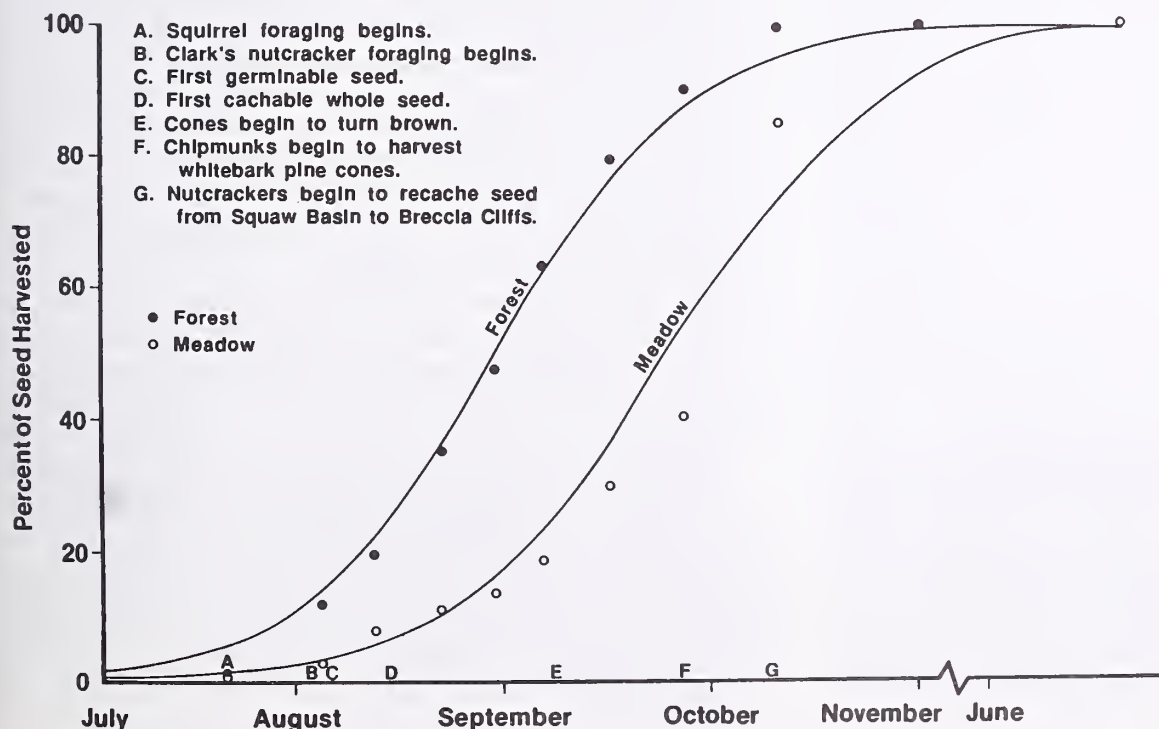


Figure 3—Seasonal course of whitebark pine seed harvest by vertebrates in Squaw Basin, WY, in 1980.

Nutcrackers were observed harvesting seed as early as July 13, 1979. During July, however, they appeared to only be testing the cones for ripeness and primarily feeding on the previous year's caches until mid-August. Seed harvested at this time were lost to regeneration because the seed coats were broken and the seed is ungerminable until August 13. In 1980, the birds were able to successfully harvest whole, developed seed by August 15. Nutcrackers harvested seed from cones at increasingly faster rates (Hutchins and Lanner 1982) through early October, when seed became hard to find (fig. 3). Nutcrackers were never seen attempting to harvest Engelmann spruce or lodgepole pine, even as the whitebark pine seed crop dwindled in October. As the seed supply became scarce in mid-October, I observed one bird checking over 50 cones for a period of 613 seconds without finding a single seed.

By November 2, it appears nutcrackers were almost totally dependent on their new seed caches, and would remain so until the following August. These caches were placed just below the soil surface (2-3 cm), and over 70 percent of the caches were either one- two- or three-seed caches ($\bar{x} = 3.2 \pm 2.8$ seeds/cache; fig. 4). The largest cache was 14 seeds. These data agree closely with Tomback (1978) and Vander Wall and Balda (1977), although the number of single-seeded caches was higher.

Clark's nutcrackers cached their seeds in almost every conceivable soil type and microsite in the various study sites. Specific examples were given in Hutchins (1990). Although they may cache seeds on a wide variety of sites in the Rocky Mountains, several studies have indicated that south-facing slopes seem to be preferred (Lanner 1982; Lanner and Vander Wall 1980; Snethen 1980; Tomback 1978; Vander Wall and Balda 1977). Seedling establishment appears to be much more common on more moist sites in the Rocky Mountains (Arno 1986; Arno and Hoff 1989; Vander Wall and Hutchins 1983) than in the Sierra Nevada (Tomback 1982).

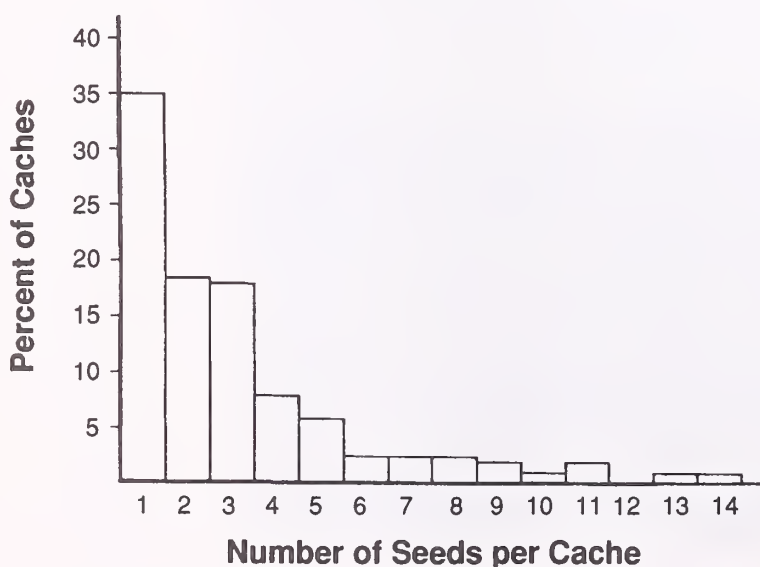


Figure 4—Clark's nutcracker cache size frequency. Data from 157 observations made at several locations in Wyoming.

Transport distances varied greatly. Seeds were placed as close as 50 m from the site of the harvested tree, or were transported at least 3.5 km to the Breccia Cliffs on the edge of the Squaw Basin site. With little seed left in the trees by mid-October, the birds began retrieving many of their caches made in the Squaw Basin meadows and recaching them on the southwest-facing slopes of the Breccia Cliffs.

Large flocks of nutcrackers would often cache seed together. At Mount Washburn, a flock estimated at 150 birds was seen caching seed under an open-grown whitebark pine stand, with 10-15 birds within a 10-m² area. No aggression occurred among the birds during these observations.

By November 2, 1980, snow covered many of the caching areas for the winter. Nutcrackers were observed on several occasions successfully pecking through up to 25 cm of snow and ice to retrieve a cache during the winter months. The Togwotee Pass area may receive up to 1,500 cm of snow a year, yet the windswept ridges and south-facing slopes remain exposed enough for the birds to retrieve their caches. Caches on the northeast-facing slopes and under the forest canopy are more frequently used during June, July, and August, as the snow recedes from these sites last (Vander Wall and Hutchins 1983).

The number of seed an individual nutcracker caches annually has been estimated in several studies. The numbers for whitebark pine range from 32,000 in the Sierras (Tomback 1982) to 98,000 in the Rocky Mountains (Hutchins and Lanner 1982). Because of the number of variables that must be considered (such as flight distances and the amount of available seed), these estimates vary a great deal from site to site and year to year.

Studies by Tomback (1982), Vander Wall (1988), and Vander Wall and Balda (1977), estimate that an individual bird caches several times more seed than it needs to survive through the winter and early spring. At that time other food items become available—although the nutcrackers continue to use their caches heavily until the new cone crop begins to mature (Vander Wall and Hutchins 1983). This leaves many unused caches for potential germination and establishment of whitebark pine seedlings (Hutchins and Lanner 1982).

Clark's nutcracker stands out from all the other potential seed dispersers in two major ways. First, it consistently disperses seed in a way that increases the chance of seedling establishment. The seed is placed just below the soil surface and hidden from seed predators (Hutchins and Lanner 1982; Lanner 1980).

Second, nutcrackers scatter caches across the landscape—both long and short distances from the source trees. Dispersal distances of up to 22 km have been observed by Vander Wall and Balda (1977). Also, the scattering of thousands of their caches reduces predation.

Steller's Jay (*Cyanocitta stelleri*)—Having many of the behavioral and physiological attributes of the Clark's nutcracker (Vander Wall and Balda 1981), the Steller's jay could have potential as a dispersal agent of whitebark pine. In this part of their range, they were found to be primarily solitary foragers and uncommon visitors to the whitebark pine forest. These birds did not forage for whitebark pine seed until early September when the

cones dried and the scales separated slightly. Their bill structure does not approach the efficiency of the nutcracker in prying apart cone scales to get to the seed (Vander Wall and Balda 1981), thus they were often only able to extract seed from cones that had been exposed by nutcrackers. These jays harvested whitebark pine seed from the ground and canopy in less than half of their observed foraging time during the fall of 1980 and 1981 (Hutchins and Lanner 1982). The seed was always placed between their feet and hammered with their bill to crack the hull; nutcrackers primarily cracked the seed between their mandibles.

Occasionally Steller's jays pouched their seed in their elastic esophagus for later caching. They were observed caching whitebark pine seeds on seven occasions; however, none of these were in the soil. The birds placed the pine seeds in the crotch of a tree, a densely foliated witches broom, and under dense lichen growth along a tree branch. The largest number of seeds I observed being pouched at one time by this species was five, although data from Vander Wall and Balda (1981) indicate these birds could hold up to 32 seeds/pouchload. Because this species does not cache whitebark pine seed in the soil and has a seed foraging rate comparable to small passerines (Hutchins and Lanner 1982), it is a very improbable agent for seedling establishment.

Raven (*Corvus corax*)—A third corvid rarely observed foraging on whitebark pine seed was the common raven. These birds had a great deal of difficulty extracting seed from whitebark pine cones due to their thick, long bills. They dropped most of the seed when foraging (Hutchins and Lanner 1982). Caching of carrion was observed with this species, but no observations were made of seed caching. In Asia, Reimers (1959 cited in Turcek and Kelso 1968) described observations of ravens caching Japanese (*Pinus pumila*) and Siberian stone pine (*P. sibirica*), although it was not clear in what type of substrate.

Other Passerines—Pine grosbeaks (*Pinicola enucleator*) primarily foraged on whitebark pine seed that had been exposed by Clark's nutcrackers breaking off cone scales. Their large conical beaks also enabled them to tear away cone scales to get at seed. Their foraging rates were very slow compared to nutcrackers due to their technique and, as a consequence, they had little influence on the depletion of the whitebark pine cone crop.

Grosbeaks are not known to cache food (Smith and Balda 1979; Vander Wall 1990). During my observations of this species, they cracked the seed coat and consumed the seed in the tree crown. It is highly unlikely that they could pass an intact seed through their digestive tract.

The mountain chickadee (*Parus gambeli*) and red-breasted nuthatch (*Sitta canadensis*) occasionally searched through the whitebark pine cones during September after the seeds were exposed by nutcrackers. Both these species almost always dropped the seed from the tree crown, as the seeds were too large for them to handle. Their unsuccessful foraging bouts contributed to the small percentage of seed found on the soil surface, which was later consumed by other animals. Neither bird species was observed caching whitebark pine seed, although they are known to

cache smaller seeded conifer species under bark (Smith and Balda 1979).

MAMMAL DISPERSERS

Red Squirrel (*Tamiasciurus hudsonicus*)—Red squirrels are common denizens of whitebark pine forests. In fact they were the second most commonly observed vertebrate next to the Clark's nutcracker (Hutchins and Lanner 1982). These mammals actively defend their territories (Smith 1968), and like nutcrackers, harvest whitebark pine cones and seeds as a fall and winter food source. Red squirrels did not occur on the meadow sites.

Red squirrels spent most of their foraging time (75.8 percent) on whitebark pine cones or recovering dropped whitebark pine seeds. This includes the time it takes to place the cones in the midden. Most of the rest of the observed foraging activities were collecting Engelmann spruce cones (11.3 percent) and harvesting seeds of herbaceous plants (12.9 percent).

Red squirrels began harvesting cones as early as nutcrackers harvested seeds (July 13, 1979), but did so more intensely during July while the nutcrackers relied more heavily on the previous year's caches (fig. 3). Their foraging rate is much higher than that of the other mammals discussed in this paper because they usually harvest entire cones. Most of the time, they remove the cone by pulling it off the branch with their teeth, instead of cutting the subtending branch (Hutchins 1990). Thus, cone removal is likely to cause little change in tree growth form or cone production.

Cone caching began on August 4 at Squaw Basin. Red squirrels often would leave cones on the ground below the tree where they were cut for periods of up to 3 days before caching them in their midden. Caching of other conifer cone species began later with Engelmann spruce on August 18 in 1980; subalpine fir (September 11 in 1980), and lodgepole pine (September 27 in 1980). All cones were stored in "middens" ($n = 114$). These middens can be quite extensive and are composed of many years of cone debris above the soil surface (Finley 1969; Reinhart and Mattson 1990; Smith 1970). Of the time spent caching food, 61.4 percent was devoted to whitebark pine cones and 16.9 percent to whitebark pine seeds. Foraging on the cones of other conifers in the subalpine made up most of the rest of the caching time (7,304 seconds of observation). Red squirrels also cached some mushrooms and herbaceous seeds.

Squirrels were also found to cache whitebark pine seeds in their midden beginning around September 16, 1980. These seed caches were placed 6.5- to 40-cm deep ($n = 6$); four of these observations were between 11 and 11.5 cm deep. The number of seeds per cache ranged from 14 to 55 ($x = 28.8$; 19.2 seeds/cache; $n = 4$), although Kendall (1981) found up to 176 seeds in a single hole. I examined the seeds from two squirrel caches and found all the seeds sound.

Red squirrels actively chased Clark's nutcrackers from the trees above their territories and their middens. On two occasions, however, I watched nutcrackers steal whitebark pine seeds from squirrel middens.

Chipmunk (*Eutamias* sp.)—Chipmunks are uncommon visitors to whitebark pine tree crowns but do occur on both open-meadow and forested sites. Most of their time is spent on the ground, usually near cover plants like sagebrush (*Artemisia tridentata*). They preferred herbaceous plant parts (lupine seed, grasses, etc.) on my subalpine study sites until the third week of September when these plants died back and presumably lost much of their nutritive value. At that time, they clumsily foraged on the remaining whitebark cone crop (~10 percent of the seed was left in the forest, ~40 percent in the meadow). They more commonly foraged on the small amount of seed below the trees, which had been dropped by any of the species discussed earlier. Tevis (1953) and Heller (1971) similarly found that in the Sierra Nevada chipmunks devote little time to foraging on whitebark pine seed and cones.

I found no evidence of chipmunks caching whitebark pine seed. Broadbooks (1958) found the larder cache depth of yellow pine chipmunks (*Eutamias amoenus*) to average 28 cm. They use these types of caches as a winter and spring food source when they are periodically aroused during hibernation (Vander Wall 1990). I examined chipmunk burrows to a depth of 20 cm without finding any evidence of them harvesting and caching whitebark pine seed.

Yellow pine chipmunks are known to scatter-hoard smaller amounts of Jeffrey pine (*Pinus jeffreyi*) and ponderosa pine (*P. ponderosa*) seed in shallower caches from 1 to 25 mm in depth (Vander Wall 1992a). These species of chipmunks in these studies, along with other rodents, may retrieve many caches in the fall in the Sierra Nevada. They use the seed to stock their winter larders, but many seeds survive and germinate the following spring (Vander Wall 1992b). Although chipmunks may play a role in the afforestation of certain pines, there are no data that support this conjecture for whitebark pine. Vander Wall (1992a) provides strong evidence that Jeffrey pine may arise from chipmunks (*Tamias amoenus*, *speciosus*, and *quadramaculatus*) scatter-hoarding seed. In Japan, Hayashida (1989) found Siberian chipmunks (*T. sibiricus*) were not an effective dispersal agent of Korean stone pine (*P. koraiensis*) in a plantation. In this study, the limited amount of seed these animals harvest (see seed crop depletion section of this paper) apparently precludes them from being of significance to whitebark pine establishment in the Rocky Mountains. More detailed observations of chipmunks in whitebark pine ecosystems are needed to more accurately define their role as cache predator and possible seed disperser.

Golden-Mantled Ground Squirrel (*Spermophilus lateralis*)—Due to a slow foraging rate and relatively rare occurrence in tree canopies, the golden-mantled ground squirrel also consumes a limited amount of whitebark pine seed. This species was found in a whitebark pine tree only once in 188 hours of observation. It does collect a limited amount of seed from the ground, which falls from cones during foraging accidents involving other animals.

Like chipmunks, ground squirrels are known to scatter-hoard shallow seed caches as well as make a deeper larder hoard (MacClintock 1970; Vander Wall 1990). This

species also begins hibernation quite early in September and would not have time to acquire much seed for storage. As with the chipmunk, few studies have been performed to define ground squirrel foraging and caching behavior.

SECONDARY DISPERSERS

Nocturnal Rodents—This group of animals, made up primarily of mice and voles (family Cricetidae), must also be considered as potential dispersal agents of whitebark pine seed. They were not directly observed in this study, but possible evidence of their foraging on whitebark pine seed was discovered by the shelled seed left behind on my simulated cache experiments.

Surface seed caches simulating the seed that was found on the ground indicate it will not last long (Hutchins 1989; McCaughey and Weaver 1990). Most of the seed in these caches was consumed within 2 weeks after placement under trees by evidence of the seed shells left behind. Almost all of the shells were left behind at the cache site, indicating little if any caching was done.

There are two primary places where cricetid rodents may obtain whitebark pine seeds: (a) from seed that falls to the ground and (b) the discovery of animal (primarily nutcracker) caches. A small amount of seed (~4 percent of the seed crop) was found to fall to the forest floor in the mast year of 1980. About 69 percent of seed found on the ground was determined unviable by examination of the contents inside the shell. Although these rodents may recache the seed, the seed was probably already placed in a suitable site for seedling establishment by a Clark's nutcracker. Thus, even if these cricetids relocate the seed to another cache, their positive effect on the establishment of whitebark pine is questionable at best.

Abbott and Quink (1970), working with the winged eastern white pine (*Pinus strobus*) seeds, showed most caches by these rodents were made less than 15 m from the seed source. Thus, the habit of whitebark pine trees pioneering open meadows and disturbed areas is highly unlikely to arise from cricetid caches. Their study also showed that of those caches not recovered by the time the seed germinated, the germinated seedlings were soon consumed by these animals. This information coupled with the small amount of seed available on the ground for these rodents suggests that they could rarely be responsible for seedling establishment. Future studies need to look at this group of dispersal agents more closely to further delineate their role in whitebark pine ecosystems.

Mice of the genus *Peromyscus* are members of this group of rodents, which is known to scatter-hoard pine seedlings (Abbott and Quink 1970; Vander Wall 1992a). Like the chipmunks and ground squirrels, this species searches for seeds on the ground and will either eat them or cache them for later use. Because so few sound whitebark seeds make it to the ground, it appears the role of these small rodents in whitebark pine establishment is insignificant.

Grizzly and Black Bears—Bears (*Ursus arctos* and *U. americana*) primarily obtain seed from squirrel middens (Kendall 1981, 1983; Mattson and Jonkel 1989), although black bears are known to also break branches to harvest the seed (Tisch 1961). Examinations of bear scat from

both species have yielded only a few intact whitebark pine seeds (Hutchins and Lanner 1982). Even if these seeds could germinate in the bear scats, they would produce an insignificant number of whitebark pine seedlings that are dispersed a very short distance from the squirrel midden the bear raided.

PERCENT OF SEED HARVESTED

On forested sites, about 63 percent of the seed was harvested by red squirrels and 36 percent by Clark's nutcracker. The other 1 percent was harvested by all other animals combined (table 1).

In contrast, on the meadow sites, which have too few trees for squirrels to exist, nutcrackers harvested almost the entire crop of whitebark pine (99 percent). Details for how these values were calculated are described in Hutchins (1982, 1990).

In all but a year with a super-abundant cone crop, animals harvest nearly all of the seed crop by early November in the Rocky Mountains (Hutchins and Lanner 1982; Vander Wall 1988). By this time, no cones remain on the trees and seeds do not have a chance to survive long enough on the ground and germinate as suggested by Day (1967) and others. In this study I found that the seed and cones that have been dropped to the ground are eaten within 3 weeks by various foragers.

CONCLUSIONS

Nutcrackers, squirrels, and the other whitebark pine seed forager guilds will occasionally drop some seed to the ground (~4 percent). Some seed is dropped intentionally (Vander Wall and Balda 1977) and some by accident. Most of this seed, however, is composed of unfilled or aborted ovules (69.5 percent) and could never germinate. Consequently, dispersal and establishment of whitebark pine by small rodents like deer mice, ground squirrels, and chipmunks would be too rare an event for a tree species to survive and prosper.

We also cannot assert red squirrels to be an establisher of whitebark pine seedlings. As I stated in earlier work, I found no evidence of whitebark pine establishing on

squirrel middens (Hutchins 1989). The midden "seed bed" is too deep in organic debris, and the activity on the midden constantly disturbs the soil.

Squirrels do harvest most of the whitebark pine seed in the forest, and they are the major seed predator on forested sites. Their midden cone stores are also important for providing grizzly and black bears with an important fall food source (Reinhart and Mattson 1990).

Nutcrackers, on the other hand, are one of the most important biotic influences developing and changing subalpine communities. This species alone probably accounts for nearly all whitebark pine regeneration, except for chance happenings. As far as the bird and the tree are concerned, it is more profitable to cache in the open meadow. Much less predation occurs on nutcracker caches in the meadow (Hutchins 1990), and the small ridges are usually free of snow due to wind action. Consequently, the higher cache survival rate benefits tree regeneration as well as the survival of the nutcracker. This more than any factor may be why we see whitebark growing where we do—pioneering the exposed ridges, roadside cuts, burned sites, and meadow swales.

The open-grown meadow trees may be the most important because the seeds from these trees will have a greater chance of being dispersed by Clark's nutcracker. These small tree islands lack the major seed predator (the red squirrel). It should be added that Reinhart and Mattson (1990) also found lower numbers of red squirrels using pure whitebark pine stands. These also may be good sources for increasing whitebark pine regeneration.

When nutcrackers forget where they placed a cache (for example, Vander Wall 1982), or die, or a rodent does not discover the seed cache—it has a chance to germinate. By placing the seed in an excellent germination bed just below the soil surface (2-3 cm) and also hiding the seed from easy discovery by seed predators, the bird may begin a new forest stand.

Eventually, these whitebark pine trees modify the once-open subalpine landscape so other more shade-tolerant species such as Engelmann spruce and subalpine fir can establish themselves in this community (Arno 1989; Franklin and Dyrness 1973; Snethen 1980). The seed and cover produced by whitebark pine attracts a large

Table 1—Estimate of whitebark pine seed harvested by various animals in Wyoming

Species	Mean seeds extracted/ minute ¹	Minutes spent foraging/ day ²	Foraging days/ season	Seeds harvested/ individual	Number of individuals visiting trees	Percent seeds harvested by all individuals	
						Forest	Meadow ³
Clark's nutcracker	7.9	180	91	129,402	448	36.3	99.4
Steller's jay	.7	120	55	4,620	11	<.1	.1
Raven	.6	30	53	954	15	<.1	<.1
Noncorvids	.7	120	56	4,704	43	.1	.3
Red squirrel	43.4	240	84	874,944	116	63.5	—
Chipmunk	1.7	120	35	7,140	10	<.1	.1

¹Seasonal average from observations made during August 15 to October 11, 1980.

²Estimate made from observed daily activity patterns.

³Meadow area lacks squirrels.

number of vertebrates (Arno and Hoff 1989; Hutchins 1990; Kendall and Arno 1990; Lonner and Pac 1990; Tomback 1978).

SUMMARY

Whitebark pine is dependent on animal dispersal for regeneration. Many animals interact with whitebark pine seed, but only Clark's nutcracker was found to consistently disperse seed in a way that leads to the regeneration of this pine. These long-distance dispersal agents should be the central focus in whitebark pine subalpine community management.

ACKNOWLEDGMENTS

I thank Steve Vander Wall for his insight on small mammals and pine seed dispersal. His comments were a great help. Susan Hutchins, Ron Lanner, and Diana Tomback helped with earlier versions of this manuscript. I thank them for their efforts.

REFERENCES

- Abbott, H. G.; Quink, T. F. 1970. Ecology of eastern white pine seed caches made by small mammals. *Ecology*. 51: 271-278.
- Arno, S. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-94.
- Arno, S.; Hoff, R. J. 1989. *Pinus albicaulis* Engelm.: whitebark pine. In: Burns, R. M.; Honkala, B. H., tech. coords. *Silvics of North America*. Vol. 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service: 269-279.
- Broadbooks, H. E. 1958. Life history and ecology of the chipmunk (*Eutamias amoenus*) in eastern Washington. Misc. Publ. 103. Ann Arbor, MI: Museum of Zoology, University of Michigan: 5-42.
- Day, R. J. 1967. Whitebark pine in the Rocky Mountains of Alberta. *Forestry Chronicle*. 43: 278-282.
- Dow, D. D. 1965. The role of saliva in food storage by the gray jay. *Auk*. 82: 139-154.
- Finley, R. B., Jr. 1969. Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Misc. Publ. 51. In: *Contributions in mammalogy*. Lawrence, KS: University of Kansas, Museum of Natural History: 233-274.
- Franklin, J. F.; Dyrness, C. T. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 417 p.
- Giuntoli, M.; Mewaldt, L. R. 1978. Stomach contents of Clark's nutcracker in western Montana. *Auk*. 95: 595-598.
- Hayashida, M. 1989. Seed dispersal by red squirrels and subsequent establishment of Korean pine. *Forest Ecology and Management*. 28: 115-129.
- Heller, H. C. 1971. Altitudinal zonation of chipmunks (*Eutamias*): interspecific aggression. *Ecology*. 52(2): 312-319.
- Hutchins, H. E. 1982. The role of birds and mammals in the dispersal and establishment of whitebark pine. Logan, UT: Utah State University. 67 p. Thesis.
- Hutchins, H. E. 1990. Whitebark pine seed dispersal and establishment: who's responsible? In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 245-255.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Kendall, K. C. 1981. Bear use of pine nuts. Bozeman, MT: Montana State University. 27 p. Thesis.
- Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. Interagency conference on bear research and management. In: *Bears—their biology and management*. Calgary, AB: International Association for Bear Management. 5: 166-173.
- Kendall, K. C.; Arno, S. F. 1990. Whitebark pine—an important but endangered wildlife resource. In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 264-273.
- Lanner, R. M. 1980. Avian seed dispersal in the ecology and evolution of limber and whitebark pines. In: *Sixth North American forest biology workshop proceedings*. Edmonton, AB: University of Alberta: 14-48.
- Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. *Canadian Journal of Forest Research*. 12(2): 391-402.
- Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. *Journal of Forestry*. 78(10): 637-639.
- Lonner, T. N.; Pac, D. F. 1990. Elk and deer use of whitebark pine forests in southwestern Montana: an ecological perspective. In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 237-244.
- MacClintock, D. 1970. *Squirrels of North America*. New York: Van Nostrand Reinhold. 184 p.
- McCaughy, W. W.; Weaver, T. 1990. Biotic and microsite factors affecting whitebark pine establishment. In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 140-150.
- Reinhart, D. P.; Mattson, D. 1990. Red squirrels in the whitebark zone. In: Schmidt, W. C.; McDonald, K. J.,

- comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 256-263.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs. 38: 31-63.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs. 40: 349-371.
- Smith, C. C.; Balda, R. P. 1979. Competition among insects, birds, and mammals for conifer seed. American Zoologist. 19: 1065-1083.
- Snethen, K. L. 1980. Whitebark pine (*Pinus albicaulis*) invasion of a subalpine meadow. Logan, UT: Utah State University. 76 p. Thesis.
- Tevis, L., Jr. 1953. Stomach contents of chipmunks and mantled ground squirrels in northeastern California. Journal of Mammalogy. 34: 316-324.
- Tisch, E. L. 1961. Seasonal food habits of the black bear in the Whitefish Range of Northwestern Montana. Missoula, MT: University of Montana. 67 p. Thesis.
- Tomback, Diana F. 1978. Foraging strategies of Clark's nutcracker. The Living Bird. 16: 123-161.
- Tomback, Diana F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51: 451-467.
- Turcek, F. J.; Kelso, L. 1968. Ecological aspects of food transportation and storage in the Corvidae. Communications in Behavioral Biology. 1: 277-297.
- Vander Wall, S. B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. Animal Behaviour. 30: 84-94.
- Vander Wall, S. B. 1988. Foraging by Clark's nutcracker on a rapidly changing pine seed source. Condor. 90: 621-631.
- Vander Wall, S. B. 1990. Food hoarding in animals. Chicago, IL: University of Chicago Press. 445 p.
- Vander Wall, S. B. 1992a. Establishment of Jeffrey pine seedlings from animal caches. Western Journal of Applied Forestry. 7(1): 14-20.
- Vander Wall, S. B. 1992b. [Personal communication]. July. Reno, NV: University of Nevada, Department of Biology.
- Vander Wall, Stephen B.; Balda, R. P. 1977. Coadaptations of Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.
- Vander Wall, Stephen B.; Balda R. P. 1981. Ecology and evolution of food-storage behavior in conifer-seed caching corvids. Zeitschrift für Tierpsychologie. 56: 217-242.
- Vander Wall, Stephen B.; Hutchins, Harry E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during the postfledging period. The Canadian Field Naturalist. 97(2): 208-214.

SIZE OF PINE AREAS IN RELATION TO SEED DISPERSAL

Hermann Mattes

Abstract—Pine seeds are either wind- or bird- (animal-) dispersed. Only well-adapted seeds support large ranges, which are of similar size in both types of dispersal. Seeds adapted to wind dispersal should have a ratio of seed weight to wing length below 1.8 mg/mm. Bird-dispersed seeds have a weight between 90 and 550 mg. Species with seeds above 100 mg but without zoochorous features have small or even relictic ranges. Large seeds are advantageous under severe conditions and in competition. Consequently, the bird-pine mutualism contributes to larger ranges of those pine species.

Distribution ranges of plant and animal species are determined by four main factors: ecological potency of the species; effectiveness of seed dispersal; size of area available; and time available. Ecological studies on plants and vegetation mostly focus on site conditions. Indeed, competition for nutrients, water, light, and so on most often turn out to be the main factor limiting distribution. However, first of all, seeds must be able to reach the site in question. Therefore, seed dispersal is an important factor in plant ecology. Patchy and irregular patterns of species on ruderal or fallow ground are a result of dissemination. Otherwise vegetation history in the Holocene gives evidence that time since last glaciation was not long enough for full expansion of all species. We expect effectiveness of seed dispersal to be correlated with rapidness of expansion and with size of range.

Small, winged seeds are easily disseminated by wind, which is present almost everywhere and anytime. Competition of the seedling within a closed vegetation cover as well as harsh environmental conditions require large seeds with a high amount of nutrient reserves. Many pine species have developed an almost obligate mutualistic relationship to birds (*Nucifraga*, *Gymnorhinus*) for seed dispersal. Pines with bird-dispersed, large seeds became dominating tree species at arctic and alpine timber lines, in xeric environments as well as in mesic lowland forests.

The genus *Pinus* with more than 100 species provides a good chance to test effectiveness of seed dispersal. All pine seeds are of a rather similar structure; the most obvious differences are seed size and wing length. The primary type is very likely an anemochorous seed with a long wing. Second, many species have developed large

seeds with shortened or missing wings. These seeds are disseminated mainly by birds, or occasionally by squirrels. Apart from that, seeds and cones show many morphological and phenological adaptations for dispersal, which are discussed elsewhere (Lanner 1980, 1982; Vander Wall and Balda 1977).

In this paper some relations of seed characteristics and size of ranges are discussed. The main hypothesis is to find the larger ranges within pine species well adapted to seed dispersal.

MATERIALS AND METHODS

From 65 out of about 106 pine species in total enough detailed information is available for a comparison of dispersal abilities and range sizes. The pine species are numbered following Mirov (1967).

Distribution ranges are of a complex nature. Effectiveness of dispersal would be measured best by the proportion of the potential area that really has been occupied by the species. Unfortunately, we do not know exactly the potential ranges of almost all plant species. An interesting idea would be to measure the distances or areas occupied after the end of the last glaciation. However, refugials and paths of dispersal are very incompletely known. What we can clearly see are area and distances within ranges. However, it seems not to be adequate to use the area of a range. It is highly influenced by size of the region (the continent or vegetation zone that is inhabited by the species concerned). Error should be less using the distance between the outermost points of a range. This was calculated as the orthodrome distance.

Split or disjunct ranges have been treated in the same way as continuous ranges. It has proved to be too difficult to decide whether an interrupted range was due to natural factors or to human influences, especially in regions that were densely populated for a long time such as East Asia and the Mediterranean.

In the present study all 105 pine species listed in Mirov (1967), and in addition *Pinus longaeva*, are considered. Subspecies have not been considered. Range maps and information was taken from Krüssmann (1968), Little (1971), Meusel and others (1965), and Mirov (1967).

In only a few experiments flying ability of pine seeds was examined (Lanner 1985; Müller-Schneider 1977). To estimate dispersal abilities of numerous species, indirect methods have been used. Simple, but reliable measurements for anemochorous seeds are weight of cleaned seeds and wing length. Such data are available for most of the species (Krüssmann 1972; USDA 1974). The ratio of seed weight to wing length is used as an indicator for potency of dispersal. Volume and surface of the seed and shape and surface of the wing would be of great interest,

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Hermann Mattes is Professor, Institut für Geographie, Abteilung Landschaftsökologie, Westfälische Wilhelms-Universität, Robert-Koch-Str. 26, W-4400 Münster, Germany.

but these data are not available for most species. Zoochorous species are even more difficult to evaluate. Seed and cone characteristics of species fully developed for bird dispersal are compared morphologically with less-adapted species.

DISPERSAL OF PINE SEEDS

Seed dispersal either by wind or by birds has caused specific adaptations. Most of the pine species can be attributed to these two main types. A narrow seed-weight to wing-length ratio is considered to be favorable to flight ability. From figure 1 with 46 pine species listed we can assume:

- In general, the length of seed wings increases until seed weight reaches about 90 mg (*P. palustris*: 93 mg/36 mm); however, the ratio of seed weight to wing length increases obviously with increasing seed weight.

- Winged seeds of more than about 100 mg have an unfavorably high ratio of seed weight to wing length; wing length is insufficient even in species with huge cones and long cone scales. These seeds are expected to have no adequate flight abilities.

- The smallest seed weight of a wingless seed species (*P. flexilis*) is 93 mg; most of the species with heavier seeds are wingless, or seed wings separate easily (*P. pentaphylla* No. 83, *P. himekomatsu* No. 84, *P. strobiformis* No. 35; also in *P. pinea* No. 73).

Comparing morphological features with area size we can conclude the following (fig. 2, table 1).

- Wind-dispersed pine species with a low ratio of seed weight to wing length often have larger distribution ranges than species with a high ratio.

- There is evidence for a log-linear relationship for the largest ranges of each class of seed weight/wing length ratio. Species with a ratio higher than 2 mg/mm are less distributed on an average. It is supposed that dispersal abilities limit the range of distribution. A remarkable exception is *P. pinea* (No. 73). Its origin is not known, and it has been cultivated in many places since Phoenician times, approximately 4,000 years ago. Therefore, the whole present range had to be taken into consideration.

- Many species do not reach an area as large as could be expected in view of their theoretical abilities for seed dispersal. This can be partly explained by geographical and ecological reasons. Species of southeastern North America (Nos. 22-31) depend on a relatively small area limited by the ocean or woodless plains. The range of Californian pines (Nos. 5, 6, 17-19) of the Mediterranean type is limited by climate. Mexican pines (seed data only for *P. chihuahuana* and *patula*, Nos. 40 and 61) also are restricted geographically and ecologically to narrow mountainous belts. *Pinus peuce* and *P. heldreichii* (Nos. 71 and 75) are endemic to the Balkan mountains in southeastern Europe.

- Ranges of bird-dispersed pines are of similar size as those of wind-dispersed pines; differences are mainly due to the very restricted range of the bird-dispersed *P. quadrifolia* in America and the huge range of wind-dispersed *P. sylvestris* in Eurasia. Some bird-dispersed pine ranges are among the largest of all pines. Concerning size of

ranges, dispersal by birds (and squirrels) is as efficient as dispersal by wind.

- Pine ranges in America are smaller than those in Eurasia. This is an effect of the larger land mass in the Old World hemisphere. Only species with well-adapted dispersal mechanisms are affected; species with relict ranges show no difference in area size.

GENUS *PINUS* DISTRIBUTION

Most of the pine species are holarctic. Pines occupy a wide variety of sites of which the most extreme are located at timber lines in cold and arid climates as well as in very dry or perhumid regions in the subtropics and tropics. Many of the pine species are restricted to specific sites. Thus, an effective dispersal agent is needed to reach suitable sites.

Recent centers of species diversity (fig. 3) are Mexico and the southwestern States of the U.S.A. Secondary centers of diversity are eastern North America, eastern Asia, and the Mediterranean region. These were refugial areas during glaciation. Although none of these areas is necessarily the origin place of the genus *Pinus*, recent regions of high species numbers of pines are assumed to be places where pines have existed for a long time.

In contrast, there are large areas populated only by a few pine species. This is the case especially in the present boreal zone. Also, we find relatively few pine species in Central America south of Tehuantepec, on the Caribbean Islands, in the Himalayas, and in southeastern Asia. Probably, these areas have been occupied by pines for only a relatively short time.

The boreal zone was reoccupied by pines in the postglacial time, and we know that some species are still expanding (for example see Gorchakovsky 1993, for *Pinus sibirica*). Nevertheless, their ranges belong to the largest ranges of pine. All boreal pine species are among the species best adapted either for wind dispersal (figs. 1 and 2; Nos. 16, 20, 21, 32, and 69) or bird dispersal (Nos. 67 and 68). Wind-dispersed pines have excellent seed-weight/wing-length ratios from 0.4 to 1.1 mg/mm.

Data are available for only a few species of southern marginal regions (*P. wallichiana*, No. 91; *P. merkusii*, No. 101; *P. khasya*, No. 104). With a ratio of seed weight/wing length of 1.2 to 1.7 mg/mm, adaptation for wind dispersal in these species is relatively good.

Species that were more widely distributed in the Tertiary or early Pleistocene, and that now occupy relict ranges only, show very different ratios of seed weight/wing length. For *P. aristata* (No. 5; 1.2 mg/mm) and perhaps *P. balfouriana* (No. 6; 2.1 mg/mm) and *P. longaeva* (No. 6a) seed dispersal might not be a restricting factor. This surely is the case in *P. torreyana* (No. 11).

Species with reduced seed wings have less chances to be dispersed by wind. Some of them are on the way to developing zoochorous features. An advanced state of zoochory shows in especially *P. strobiformis* (No. 35), and somewhat less in *P. pentaphylla* (No. 83) and *P. himekomatsu* (No. 84) (Hayashida 1989); they have large seeds and wings that easily separate from the seed. These species are already mainly disseminated by birds and animals. *Pinus peuce* (No. 71) has a small seed (40 mg) and

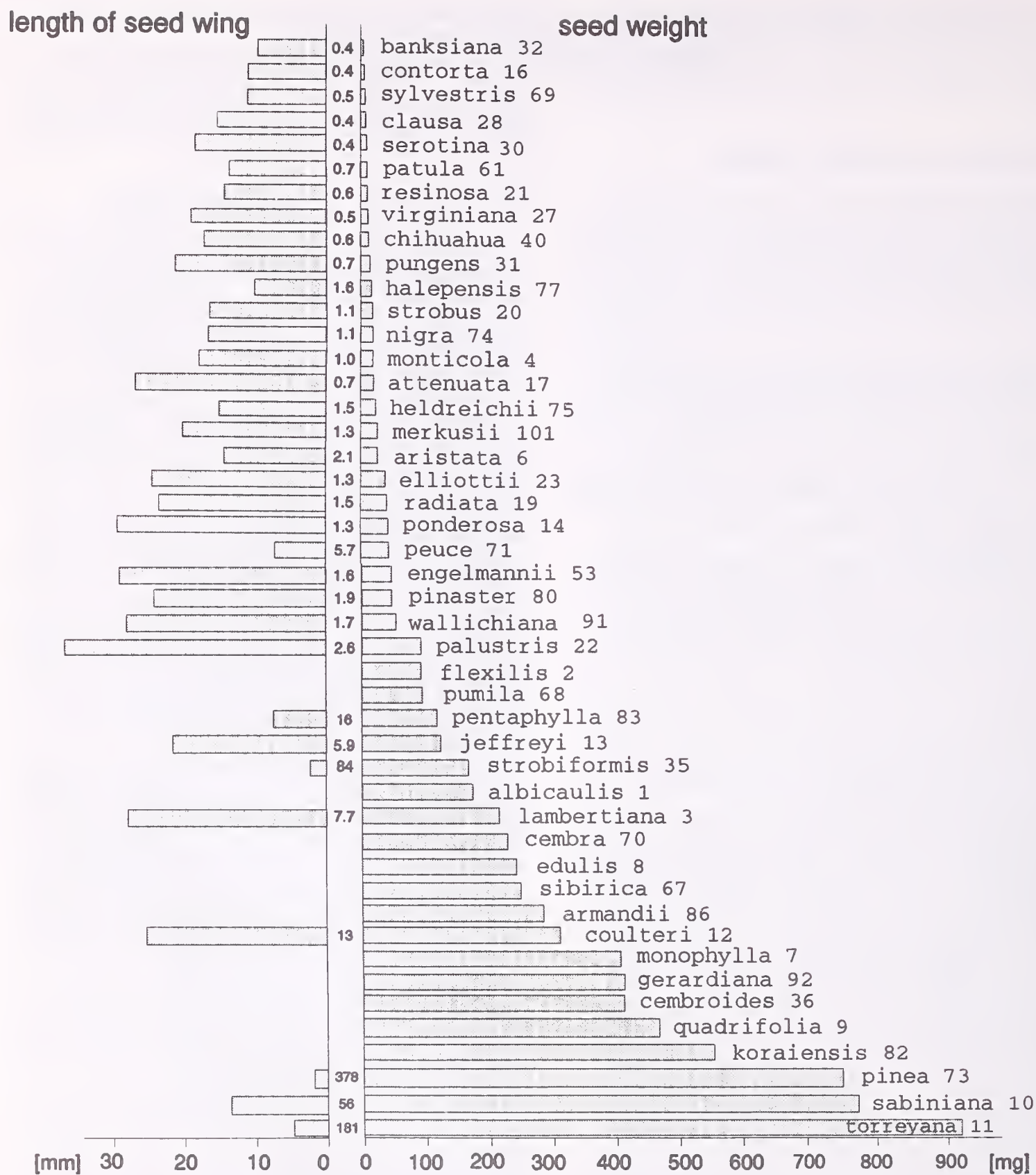


Figure 1—Wing length (mm, left), weight (mg, right), and ratio of wing length to weight (mm/mg, middle) of seeds of 46 pine species. Numbers following species names according to Mirov (1967). For sources see text. Species are arranged according to seed weight.

is not very attractive for nutcrackers, although it is used for hoarded food sometimes as is *P. longaeva* (Lanner 1988). It is assumed that dispersal by nutcrackers is of some relevance in establishing these two species at timberline. Ranges of both species are small.

Other pine species such as *P. lambertiana*, *P. sabiniana*, *P. torreyana*, *P. coulteri*, and *P. jeffreyi* (Nos. 3, and 10-13) have large seeds but lack further adaptations for dispersal by birds and animals. Since these species have no effective dispersing agent, their ranges are relatively small.

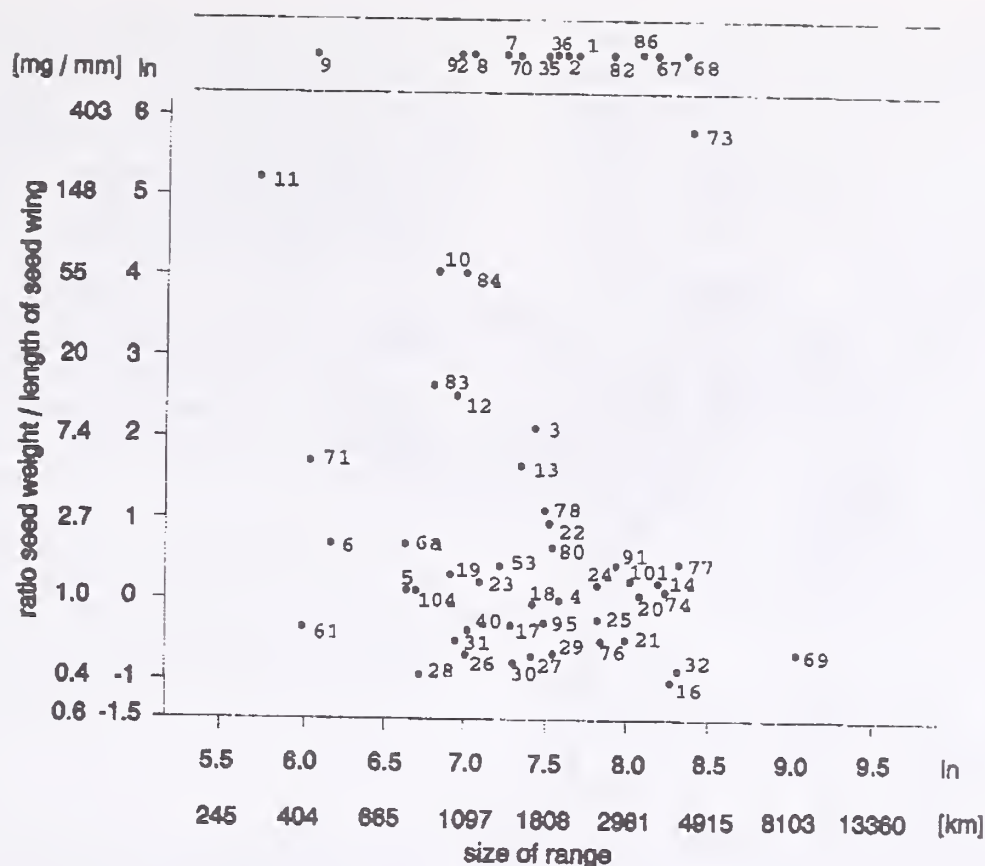


Figure 2—Size of ranges in relation to the ratio wing length/seed weight of 44 wind-dispersed pines; for comparison, range size of 13 bird-dispersed pine species on top of the figure. For code numbers for pine species see appendix; for sources see text.

Pinus pinea, as mentioned earlier, is an exception because it has been cultivated throughout history.

CONCLUSIONS

Competition in seedlings causes a high selective pressure for large seeds. Even among wind-dispersed pines seed size tends to enlarge despite a strong negative effect on dispersal ability. Obviously, at 90 to 100 mg seed weight dispersal success by wind has diminished so far that other agents are essential. From 24 haploxyton pine species, 19 species have wingless or almost wingless and

large seeds, which are proven to be or expected to be bird dispersed. There is no doubt that zoochory has developed in parallel in several sections of haploxyton pines (Lanner 1989; Tomback and Linhart 1990). Three diploxyton species (*P. torreyana*, No. 11; *P. sabiniana*, No. 12; *P. pinea*, No. 73) have large, nearly wingless seeds but lack further adaptations for zoochory.

Range sizes of bird-dispersed pines are not obviously different from those of wind-dispersed pines. Dissemination of pine seeds by birds is at least as effective as wind dispersal. The interaction of pines and nutcrackers or jays is well balanced. Even scattered stands of zoochorous

Table 1—Average size of ranges (km distance) of pine species with different dispersal agents. Wind-dispersed pines are arranged according to their seed characteristics (seed weight/wing length in mg/mm)

Pine species dispersed by:	Distribution ranges		
	America	Eurasia	Global
Birds	1,557 (<i>n</i> = 7)	2,680 (<i>n</i> = 6)	2,075 (<i>n</i> = 13)
Wind (0.4-0.8 mg/mm)	1,913 (<i>n</i> = 13)	¹ 4,247 (<i>n</i> = 3)	2,351 (<i>n</i> = 16)
Wind (0.9-2.0 mg/mm)	1,926 (<i>n</i> = 9)	2,610 (<i>n</i> = 7)	2,225 (<i>n</i> = 16)
Wind (>2.0 mg/mm)	1,121 (<i>n</i> = 7)	² 1,055 (<i>n</i> = 4)	² 1,097 (<i>n</i> = 11)
Species considered above	1,693 (<i>n</i> = 36)	² 2,566 (<i>n</i> = 20)	² 1,994 (<i>n</i> = 57)
All species	1,413 (<i>n</i> = 67)	1,779 (<i>n</i> = 39)	1,548 (<i>n</i> = 106)

¹Without *P. sylvestris*, average range size is 2,150 km.

²Numbers without *P. pinea*.

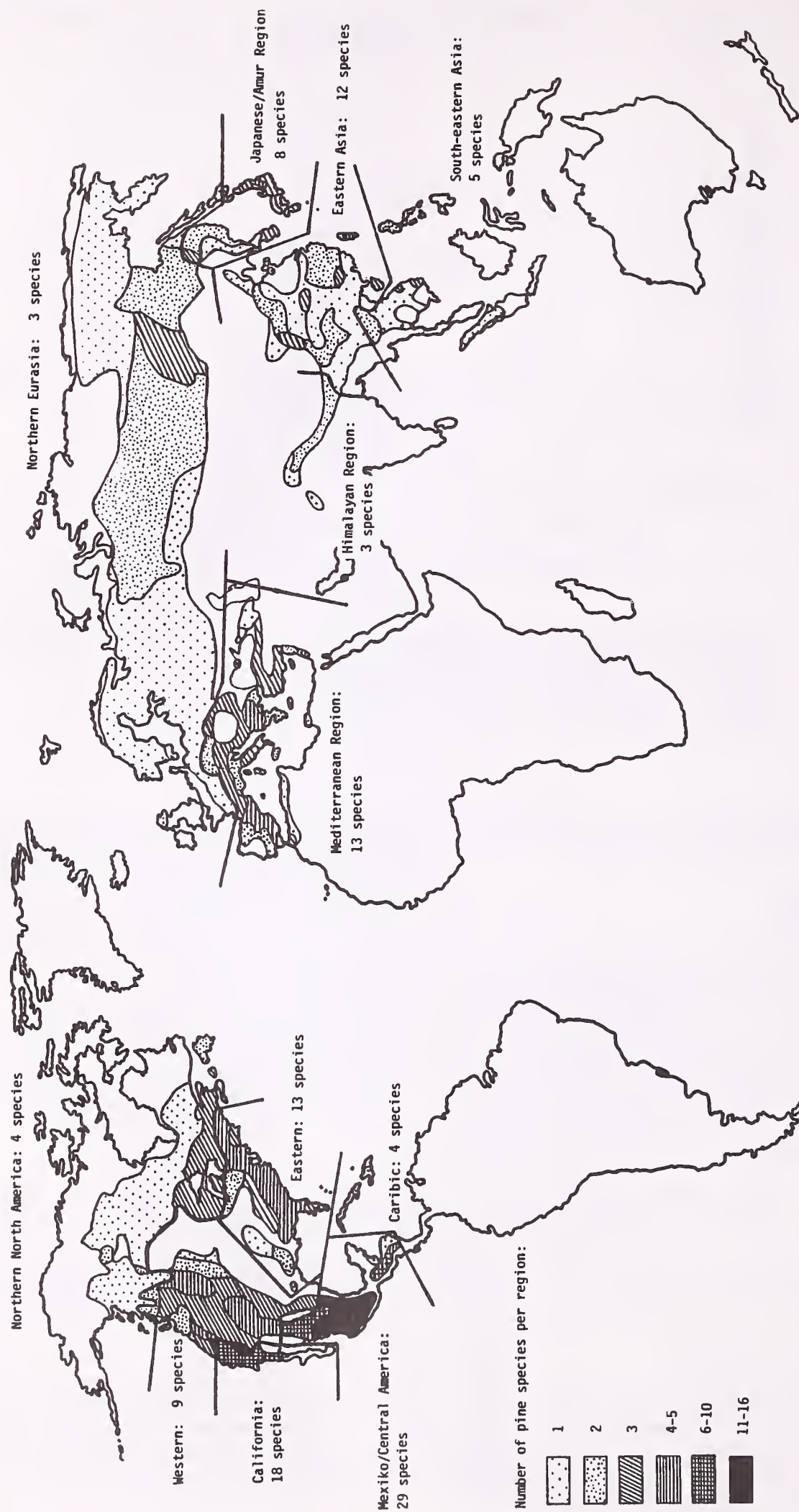


Figure 3—Distribution of the genus *Pinus* showing regional species diversity; zones of intergradation or small overlapping areas of vicarious species are not considered. Additionally, border lines and summarized species numbers of main pine regions are given.

pine trees support all needs for territories of nutcrackers concerning breeding, feeding, overwintering, and social life. Nutcrackers and jays have still preserved characteristic euryoecious features of corvids, especially omnivory. In Eurasia, where there is almost no other animal competing with the nutcracker for seed hoarding, the range of the nutcracker surpasses the ranges of zoochorous pines in many regions.

Within wind-dispersed pines we find that large-sized ranges suppose small seeds with a ratio of weight to wing length below approximately 1.8 mg/mm, but not vice-versa because of geographical barriers or specialized features of a species. However, pine species with a very high ratios of seed weight/wing length (above 1.8 mg/mm) always have restricted areas.

Altogether, pine seed dispersal by birds was very successful during evolution. Pine species became able to occupy additional and more different sites, as well as under extreme conditions at the borders of tree growth as under mesic conditions. Consequently, bird-dispersed pines were able to enlarge their ranges.

REFERENCES

- Critchfield, William B.; Little, Elbert L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Gorchakovskiy, P. L. 1993. Distribution and ecology of Siberian stone pine (*Pinus sibirica*) in the Urals. (These proceedings).
- Hayashida, Mitsuhiro. 1989. Seed dispersal and regeneration patterns of *Pinus parviflora* var. *pentaphylla* on Mt. Apoi in Hokkaido. Research Bulletin of the College Experiment Forests, Faculty of Agriculture, Hokkaido University. 46(1): 177-190.
- Krüssmann, Gerd. 1968. Die Bäume Europas. Berlin and Hamburg: Parey Verlag. 140 p.
- Krüssmann, Gerd. 1972. Handbuch der Nadelgehölze. Hamburg und Berlin: Parey-Verlag.
- Lanner, Ronald M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. Proc. 6th North American Forest Biology Workshop, University of Alberta, Edmonton, Canada: 15-48.
- Lanner, Ronald M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12(2): 391-402.
- Lanner, Ronald M. 1985. Effectiveness of the seed wing of *Pinus flexilis* in wind dispersal. Great Basin Naturalist. 45(2): 318-320.
- Lanner, Ronald. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevation. Arctic and Alpine Research. 20(3): 358-362.
- Lanner, Ronald M. 1989. Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.
- Little, Elbert L., Jr. 1971. Atlas of United States trees. Vol. 1: Conifers and important hardwoods. Misc. Publ. 1146. Washington, DC: U.S. Department of Agriculture. 9 p. and 200 maps.
- Meusel, H.; Weinert, E.; Jäger, E. 1965. Vergleichende Chorologie der zentraleuropäischen Flora. Bd. I. Jena: Fischer-Verlag. 9 p. and 200 maps.
- Mirov, Nicholas T. 1967. The genus *Pinus*. New York: Ronald Press. 602 p.
- Müller-Schneider, Paul. 1977. Verbreitungsbiologie (Diasporologie) der Blütenpflanzen. Veröffentlichungen des geobotanischen Institutes der ETH Zürich, Stiftung Rübél. Vol. 61. 226 p.
- Tombac, Diana F.; Linhart, Yan B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219. U.S. Department of Agriculture, Forest Service. 1974. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC. 838 p.
- Vander Wall, Stephen B.; Balda, Russ P. 1977. Coadaptations of the Clark's nutcracker and the pinyon pine for efficient harvest and dispersal. Ecological Monographs. Durham. 47(1): 27-37.

APPENDIX: CODING LIST OF NUMBERS OF PINE SPECIES CONSIDERED (AFTER MIROV 1967)

Western North America

Haploxyton pines

- 1 *albicaulis*
- 2 *flexilis*
- 3 *lambertiana*
- 4 *monticola*
- 5 *balfouriana*
- 6 *aristata*
- 6a *longaeva*
- 7 *monopylla*
- 8 *edulis*
- 9 *quadrifolia*

Diploxyton pines

- 10 *sabiniana*
- 11 *torreyana*
- 12 *coulteri*
- 13 *jeffreyi*
- 14 *ponderosa*
- 16 *contorta*
- 17 *attenuata*
- 18 *muricata*
- 19 *radiata*

Eastern North America

Haploxyton pines

- 20 *strobus*

Diploxyton pines

- 21 *resinosa*
- 22 *palustris*
- 23 *elliotti*
- 24 *taeda*
- 25 *echinata*
- 26 *glabra*
- 27 *virginiana*
- 28 *clausa*
- 29 *rigida*
- 30 *serotina*
- 31 *pungens*
- 32 *banksiana*

Mexico

Haploxyton pines

- 35 *strobiformis*
- 36 *cembroides*

Diploxyton pines

- 40 *chiuahuahua*
- 53 *engelmanni*

Northern Eurasia

Haploxyton pines

- 67 *sibirica*
- 68 *pumila*

Diploxyton pines

- 69 *sylvestris*

Mediterranean Region

Haploxyton pines

- 70 *cembra*
- 71 *peuce*

Diploxyton pines

- 73 *pinca*
- 74 *nigra*
- 75 *heldreichii*
- 76 *montana* (=mugo)
- 77 *halepensis*
- 78 *brutia*
- 80 *pinaster*

Eastern Asia

Haploxyton pines

- 82 *koraiensis*
- 83 *pentaphylla*
- 84 *himekumatsu*
- 86 *armandi*
- 91 *wallichiana* (=griffithi)
- 92 *gerardiana*

Diploxyton pines

- 95 *densiflora*
- 101 *merkusii*
- 104 *hasya*

THE REGENERATION PROCESS OF WHITEBARK PINE

Ward W. McCaughey

Abstract—Whitebark pine (*Pinus albicaulis* Engelm.) regenerates similarly to European and Asian stone pines. Our knowledge of this process is essential because whitebark pine is important to the North American grizzly bear (*Ursus arctos horribilis*), other wildlife species, hydrology of high-elevation ecosystems, and esthetics. This paper summarizes available information on the whitebark pine regeneration process, beginning from bud initiation through germination and seedling survival. Major factors limiting germination and regeneration success are discussed. We continue to gain knowledge about the regeneration process of whitebark pine, but further research is needed to fully understand delayed germination mechanisms and habitat requirements for optimum regeneration success.

Whitebark pine (*Pinus albicaulis* Engelm.) is an important food source for the endangered grizzly bear (*Ursus arctos horribilis*), red squirrels (*Tamiasciurus hudsonicus*), the Clark's nutcracker (*Nucifraga columbiana* Wilson), and a multitude of other birds and mammals (Hutchins and Lanner 1982; Kendall 1983; Knight and others 1987). It is also significant as a hydrologic stabilization plant and an esthetic feature of high-elevation communities (Schmidt and McDonald 1990). It provides important cover for wildlife and is used as an ornamental for landscaping but has only minor significance as a timber producing species (McCaughey and Schmidt 1990).

General information is available and is summarized in this paper on the natural regeneration process of whitebark pine, but more specific facts are needed for efficient management of this North American stone pine (Arno and Hoff 1989; McCaughey and Schmidt 1990). This paper describes the regeneration process beginning from bud initiation through germination and seedling survival.

CONE AND SEED DEVELOPMENT

Whitebark pine cone and seed development begins with cone initiation and ends with seed maturation. Climatic conditions influence the timing of development and maturation of cone initiation and seed maturation.

Cone Initiation

The process of cone initiation and development of staminate and ovulate strobili for whitebark pine has not been

specifically studied. Mirov (1967) and Krugman and Jenkinson (1974) provided generalized descriptions of the initiation process for the genus *Pinus*. Female and male cone initiation of whitebark pine probably occur during or just prior to winter bud formation from mid-August to mid-September (Schmidt and Lotan 1980).

Cone Development

Female and male buds overwinter and begin further development and growth in April and May depending on elevation. In 1992, staminate cones matured and shed pollen during June and early July at high elevations (2,500-2,600 m) in southwestern Montana (McCaughey 1992) and in May and June at lower elevations (1,550-1,650 m) in northern Idaho (Hoff 1992). Mature male cones are about 1 cm wide by 1 cm long and female cones are 1 cm wide by 2 cm long during early development when they are pollen receptive. After pollination female cones grow to a first-year size of about 3 cm long by 2 cm wide. Female cones remain on the tree, while male cones fall off after pollen dispersal. Pollination occurs from late June to late July, and fertilization occurs about 12 to 13 months later, simultaneous with rapid cone enlargement during June and July (Krugman and Jenkinson 1974).

Seed Maturation

Following fertilization the embryo develops and differentiates into cotyledons, plumule, and radicle (Mirov 1967). Whitebark seeds reach maturity between mid-August and mid-September depending on elevation and climatic conditions during the ripening process (Krugman and Jenkinson 1974; McCaughey, in press a). The entire process from cone initiation to cone and seed maturity takes about 24 months.

Cone and Seed Insects and Diseases

Whitebark pine cones and seeds are exposed to insects and disease that reduce cone and seed survival during the 2 years of development (Edwards 1990). Cone and seed insects that damage whitebark pine are cone worms (*Dio-ryctria* spp. and *Eucosma* spp.), cone beetles (*Conophthorus* spp.) (Bartos and Gibson 1990), and midges and seed chalcids (*Megastigmus* spp.) (Dewey 1989). *Siroccocus strobilinus* Preuss is a seed-borne disease that kills whitebark pine seedlings in nurseries and in natural stands. *Calocypha fulgens* (Pers.) Boud. (anamorph = *Geniculodendron pyriforme* Salt), referred to as a seed or cold fungus, may cause preemergence seed loss (Hoff and Hagle 1990). Pre- and postemergence damping-off diseases (*Fusarium* spp.) may cause extensive mortality, especially in slowly emerging seedlings (Landis and others 1990).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Ward W. McCaughey is a Research Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Bozeman, MT 59717-0278.

SEED DISPERSAL

Whitebark pine cones are well suited to the Clark's nutcracker, a forest bird that is the major disperser of whitebark pine seeds (Arno and Hoff 1989; Hutchins and Lanner 1982; Lanner 1980; Lanner and Vander Wall 1980; McCaughey and Schmidt 1990; Tomback 1982).

Cone Attributes

Unlike other conifers such as western white pine (*Pinus monticola* Dougl.) and limber pine (*Pinus flexilis* James), whose cone scales fully open to release seed, whitebark pine cone scales only open partly. The scale base does not break away from the cone axis; the wingless seeds are held firmly in place yet fully exposed and easily accessible to nutcracker extraction (Eggers 1986; Hutchins and Lanner 1982). Nutcrackers have strong, pointed bills like other species of the family Corvidae. Upper portions of the cone scales are easily broken by nutcrackers along a thin fracture zone where the massive apophysis tapers to a thin cross section beneath the seed-bearing cavities (Lanner 1982). A nutcracker can store over 100 whitebark pine seeds in its sublingual pouch, a saclike modification on the floor of the mouth (Bock and others 1973).

Nutcracker Caching

Whitebark pine regeneration depends almost entirely on nutcracker seed selection and caching habits. A nutcracker appears to discriminate between good, aborted, insect-infected, or diseased seeds by rattling each seed in its bill before depositing it in the sublingual pouch (Hutchins and Lanner 1982; Tomback 1978; Vander Wall and Balda 1977). Whitebark pine seeds are dispersed by nutcrackers up to 22 km from their source. Caches are buried 2 to 4 cm deep with 1 to 25 or more seeds per cache (fig. 1) (Tomback 1978; Vander Wall and Balda 1977). One nutcracker can store an estimated 22,000 to 98,000 whitebark pine seeds each year when seed is available (Hutchins and Lanner 1982; Tomback 1978; Vander Wall and Balda 1977). Estimates of food requirements indicate that nutcrackers may store three to five times as many seeds as needed (Tomback 1983).

Secondary Dispersers

Nutcrackers compete with other seed consumers for whitebark pine seeds. Red squirrels harvest cones and seeds from mid-July to early November, greatly reducing the availability of seed for nutcrackers (Eggers 1986; Hutchins and Lanner 1982; Reinhart and Mattson 1990; Smith 1968). Squirrels store cones in middens and seeds in caches on the forest floor (Hutchins and Lanner 1982; Reinhart and Mattson 1990).

Grizzlies obtain whitebark pine seeds primarily from squirrel middens (Kendall 1983). Germination probability from squirrel-cached cones and seed is low due to their deep caching habits (>7 cm) and small numbers of midden sites. Hypocotyl growth of whitebark pine is only 3 to 4 cm; emergence of cotyledons above the soil surface in a



Figure 1—Nutcracker cache site with five whitebark pine germinants growing on a litter seedbed near a log.

squirrel midden is unlikely (Lanner 1982). Squirrels feed on the cones and seed during the winter and spring months thus constantly disturbing the middens (Lanner 1982).

Many other animals feed on whitebark pine seed and are considered secondary dispersers because of the low probability of germination following their feeding and caching (Hutchins and Lanner 1982; McCaughey and Schmidt 1990). Other common animals that harvest whitebark pine seed either from the cones directly or indirectly from the ground or other animal caches are: birds—William's sapsucker (*Sphyrapicus thyroideus*), hairy woodpecker (*Picoides villosus*), white-headed woodpecker (*P. albolarvatus*), mountain chickadee (*Parus gambeli*), white-breasted nuthatch (*Sitta carolinensis*), Cassin's finch (*Carpodacus cassinii*), red crossbill (*Loxia curvirostra*), pine grosbeak (*Pinicola enucleator*), Steller's jay (*Cyanocitta stelleri*), raven (*Corvus corax*), and red-breasted nuthatch (*Sitta canadensis*). Mammals—chipmunks (*Eutamias* spp.), deer mouse (*Peromyscus maniculatus*), golden-mantled ground squirrel (*Spermophilus lateralis*), southern red-backed vole (*Clethrionomys gapperi*), chickaree (*Tamiasciurus douglasi*) (Hutchins and Lanner 1982; McCaughey and Schmidt 1990), and black bears (*Ursus americanus*) (Craighead and others 1982; Kendall 1983). Secondary dispersers not only reduce the seed crop but limit the availability of seed to nutcrackers and thus the probability of regeneration.

Usually whitebark pine cone crops are depleted by cone and seed consumers. Hutchins and Lanner (1982) described a 3-year period when no whitebark pine cones fell to the ground other than by animal clipping. In contrast, so many cones were produced in 1989 that many were not utilized by seed consumers and fell to the ground (McCaughey and others 1990). Grizzly bears were observed foraging on these cones in 1990 (Reinhart 1990). The 1989 mast year may have reached the upper limit of

cone production, a level that rarely occurs. Wind storms may have dislodged the whitebark cones making them available to ground foraging animals.

The probability of germination is low from seeds that have fallen to the ground in cones or been dropped by animals. All whitebark pine seeds sown on the ground are eaten or taken by seed consumers when not protected with exclosures (McCaughey 1990). This situation occurred in two successive seasons when seeds were sown during field germination tests. Eight species of rodents were trapped on site during the field germination test. The two most abundant species were the deer mouse and the southern red-backed vole representing 54 and 23 percent of the total population trapped (McCaughey 1990).

GERMINATION

Information on seed storage and laboratory germination of whitebark pine seeds, under a variety of seed treatment methods, has been summarized and discussed by several authors in the symposium proceedings "Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource" (Schmidt and McDonald 1990). The following sections extract pertinent information from those various sources.

Seed Storage

Whitebark pine seed has been frozen under environmentally controlled conditions for up to 20 years (Schubert 1954). Seed viability decreased over that time period from 50 percent to 3 percent. Mirov (1946) found that viability of whitebark pine seed dropped from 24 percent at time of collection to 17 percent after being frozen for 8 years, but dropped to 1 percent after 11 years of storage. Viability of whitebark pine seed, as related to storage time, is dependent on seed maturity when harvested, seed handling prior to storage, and methods and length of time of stratification for germination tests (McCaughey and Schmidt 1990).

Controlled Germination

Viability of whitebark pine seed, even under controlled conditions, is highly variable, ranging from 0 to 75 percent. One procedure for germinating whitebark pine seeds is to soak seeds in running tap water for 1 to 2 days and stratify moist at 1 to 5 °C for 90 to 120 days in plastic bags (Krugman and Jenkinson 1974). Stratification time may vary by seed maturity. Jacobs and Weaver (1990a) found that 1 month of stratification was sufficient to increase germination from 5 percent to about 40 percent; longer stratification periods (to 8 months) did not improve germination. The Coeur d'Alene Nursery in Idaho, U.S.A., used the following procedures for germination tests for western white pine and whitebark pine:

- A. Place seed in nylon mesh bags.
- B. Soak seed for 48 hours in running tap water. Place nylon mesh bag in plastic bag.
- C. Stratify for 100 days at 1 to 2 °C. Within that 100-day stratification time resoak the seed for 1 hour each week.

D. After 100 days, remove seed from stratification and surface dry.

E. Using a vacuum seeder, place 100 seeds on moist paper towels (Kimpak) in each of four plastic trays.

F. Place trays in germinator and take counts.

Seedling Morphology

Whitebark pine germinants have thicker stems than those of associated conifers. Stem diameters range from 2 to 4 mm for whitebark and only 1 to 2 mm for lodgepole pine (*Pinus contorta* var. *latifolia*), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (McCaughey 1988). Germinants produce five to 12 cotyledons and grow to heights of 3 to 5 cm in the first growing season (fig. 2) (McCaughey and Schmidt 1990). Needles vary in length from 7 to 10 cm with stomata positioned on the dorsal and ventral sides. The hypoderm is weak, usually one cell in width; the endodermis has an outer wall that is strongly thickened, and there is only one fibrovascular bundle (Harlow 1931).

Whitebark pine trees commonly have multiple stems from forking of a single stem or the merging of several seedlings from a nutcracker cache. Forking occurs on a small percentage of whitebark pine germinants. Nearly 7 percent of first-year germinants have two forks and 17 percent have three or more forks (McCaughey 1988; Weaver and Jacobs 1990). Genotypic analyses of multi-stemmed clumps show that 58, 70, and 83 percent, of three stands sampled in Alberta, Canada, and Wyoming, U.S.A., had stems of mixed genetic origin while 42, 30,



Figure 2—Single whitebark pine seedling germinating on a mineral seedbed and showing newly emerged cotyledons.

and 17 had arisen by branching (Furnier and others 1987; Jacobs and Weaver 1990b; Linhart and Tomback 1985). This indicates that trees of mixed genetic origin had merged from several genetically individual seedlings from the same cache.

Whitebark pine germination and root growth are affected by early season soil temperatures. Seeds germinate when soil temperatures are between 10 and 40 °C with an optimum temperature range of 25 to 35 °C (Jacobs 1989; Jacobs and Weaver 1990a). Root growth occurs between 10 and 45 °C with the optimum temperature range being 25 to 35 °C. This optimum range provides conditions where whitebark roots grow 5 to 15 mm per day (Jacobs and Weaver 1990a). First-year root growth ranges between 5 and 18 cm for nutcracker-cached seedlings growing in a forest environment (McCaughey 1988).

Period of Germination

Germination from a single sowing or caching of whitebark pine seeds can continue throughout the growing season and during the next 2 to 3 or more years (McCaughey, in press b). Because nutcrackers bury seed 2 to 4 cm deep, seeds may germinate but not emerge above the soil surface for several days after germination or they may not emerge at all. The term germinant in this paper refers to an emergent, since it is difficult to discern if a seed germinated yet died prior to emergence.

Germination Sites

Whitebark pine germinates on a variety of seedbeds, almost entirely dependent on the choice of the nutcracker. Whitebark pine grows within 38 habitat-phase combinations in eastern Idaho and western Wyoming (Steele and others 1983) and 44 in Montana (Pfister and others 1977). Typical sites for Clark's nutcracker caches are well-drained and moist substrates, bare soil, forest litter, gravel, rubble, in small plants and logs, in cracks and fissures on exposed rock, and in pumice soils (Hutchins and Lanner 1982; Tomback 1978, 1982; Tomback and others 1990). Regeneration is commonly found on burned litter seedbeds following natural and prescribed burns (Morgan and Bunting 1990; Tomback 1986).

Nutcrackers cache whitebark seeds on all aspects, but the majority of cache sites occur on southeast, south, southwest, and west-southwest aspects (Tomback and others 1990). Seed storage in south-aspect windblown sites probably ensures that some caches are snowfree in winter and spring so the nutcracker can retrieve them. Even though fewer seeds are cached on the north aspects, regeneration densities are highest on north aspects. This may be due to less successful retrieval by the nutcracker, or it may be a result of favorable environmental conditions such as moisture and insolation protection during the germination period (Tomback and others 1990). The tallest and best formed whitebark pine trees are often found in high basins or on gentle north slopes (Arno and

Hoff 1989). Drought and insolation mortality of seedlings on south slopes may contribute to the disproportionate success of whitebark regeneration on north aspects.

First-Year Germination

Whitebark pine seed germinating from caches by the nutcracker begins about mid-June and continues through early September. The number of whitebark pine seeds germinating in the first year after caching varies by year, probably in response to timing of spring snowmelt and early summer rains (fig. 3) (McCaughey 1990). For example, in 1988 only 11.5 percent of buried seeds germinated, probably due to below-average precipitation (82 percent of normal). In 1989 precipitation was near normal and germination of 1988 sown seed was nearly 34 percent (table 1) (McCaughey 1990).

First-year germination of whitebark pine is significantly affected by percent shade cover (0, 25, and 50 percent), seedbed condition (mineral, litter, and burned), and sowing depth (surface sown and buried) (table 1) in controlled field studies in southwestern Montana, U.S.A. (McCaughey 1990). Percent germination of whitebark pine was significantly ($p = 0.008$) higher (20.4 percent) under a 50 percent shade cover than with no shade (16.7 percent) (table 1) (McCaughey 1990). Germination of whitebark pine seeds sown in 1988 was 26 percent on mineral seedbeds and significantly less on litter and burned seedbeds, 14.5 and 15.3 percent, respectively (McCaughey 1990). Buried whitebark pine seeds (2 to 4 cm deep) had significantly higher germination in 1988 and 1989 (11.5 and 33.7 percent, respectively) than surface-sown seeds that were protected from seed consumers in the same years (1.8 and 11.5 percent, respectively) (McCaughey 1990).

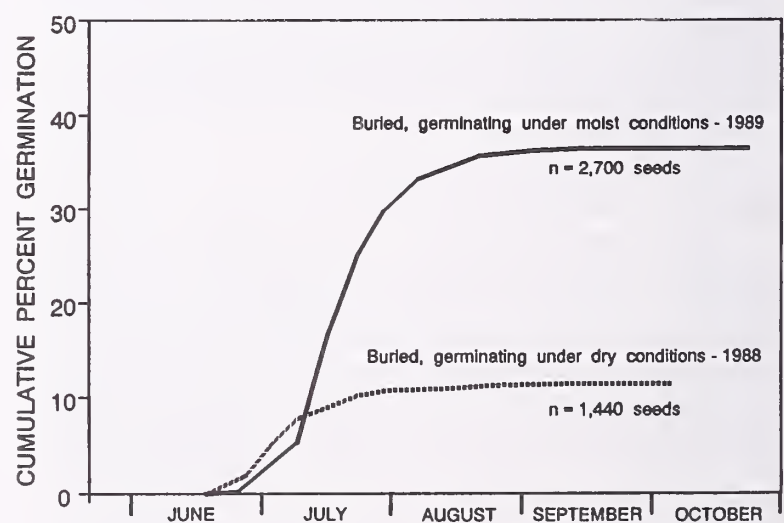


Figure 3—Cumulative percent germination of whitebark pine germinants from buried and protected seeds, sown in 1987 and 1988 respectively, germinating under dry (1988) and moist (1989) conditions. Data collected from a clearcut at 2,530 m elevation in southwestern Montana, U.S.A.

Table 1—Percent first-year germination of 1987 and 1988 sown seeds of whitebark pine as affected by shade cover, seedbed condition, and sowing depth. All treatments excluded seed consumers allowing for surface germination. Data collected from a clearcut at 2,530 m elevation in southwestern Montana, U.S.A.

Factor	Factor level	First-year germination	
		1988 mean	1989 mean
----- <i>Percent</i> -----			
Shade cover (percent)	0	15.2 (a)	16.7 (c)
	25	7.9 (a)	18.8 (cd)
	50	6.8 (a)	20.4 (d)
Seedbed condition	Mineral	8.2 (a)	26.0 (c)
	Litter	5.1 (b)	14.5 (d)
	Burned	—	15.3 (d)
Sowing depth	Surface	1.8 (a)	3.5 (c)
	Buried	11.5 (b)	33.7 (d)

¹Similar and dissimilar letters in parentheses within a column for a factor represent nonsignificant and significant differences respectively.

Delayed Germination

Delayed germinants are whitebark pine seeds that germinate two or more seasons after being sown or cached. The European stone pine (*Pinus cembra*) germinates in the first, second, and third year after caching (Krugman and Jenkinson 1974). Whitebark pine seed germinates at least 3 years following sowing (McCaughey 1990; McCaughey, in press b; McCaughey and Schmidt 1990). Although there were absolute value differences, the effects of shade cover and seedbed condition became nonsignificant as germination occurred over a 3-year period in a study of whitebark germination in western Montana, U.S.A. (table 2) (McCaughey, in press b). Germination from buried seed (56 percent) remained significantly higher than for surface-sown seed (7 percent) 3 years after sowing (McCaughey, in press b).

Dormancy of whitebark pine seed is caused by embryo underdevelopment, physiological embryo dormancy, imperviousness of the seed coat and female gametophyte tissue to oxygen and water uptake, and possibly by deposition of growth inhibitors to the embryo by female gametophyte tissue (Pitel 1981; Pitel and Wang 1980, 1990). Seeds of whitebark pine must mature in a short growing season in high-elevation forests, and if climatic conditions slow the maturation process nutcrackers will harvest immature seed. Nutcrackers are normally not concerned with seed maturity and will also harvest seeds early in the season before they are mature. Embryo underdevelopment can be overcome by exposing imbibed seeds to 20 °C for 30 to 60 days (Leadem 1985). Clipping the seed-coat is a method to overcome physiological barriers to germination (Pitel 1981).

Under natural conditions, the greatest germination from cached whitebark pine seeds occurs in the second

year following caching due to delayed dormancy mechanisms (McCaughey 1990, 1992; Tomback 1992). For example, germination of buried whitebark pine seed increased from 11 percent in the first year following sowing to 45 percent in the second year. Germination declined to 11 percent in the third year following sowing (McCaughey, in press b).

Limiting Factors

Germination rates for whitebark pine are highest from mid-June through the end of July (McCaughey 1990). Mortality of first-year seedlings follows the same pattern; the highest mortality rates occur when germination is highest (fig. 4) (McCaughey 1990). Germination exceeds mortality up to the first of August, resulting in an accumulation of surviving seedlings; however, germination and mortality rates decrease after the first of August. Germination continues from early August until the first of September with total numbers of survivors remaining constant because mortality equals germination (McCaughey 1990). Late germinants have the same probability of survival as early germinants. Factors limiting seedling survival include:

Microsite and Biotic—Three major factors are: (1) insolation (heat scorching of seedling stem at ground surface), (2) drought (drying out of seedling), and (3) animals (burial, uprooting, or nipping), specifically pocket gophers (*Thomomys talpoides*) (McCaughey and Schmidt 1990). Hutchins and Lanner (1982) observed a chipmunk uproot and consume a whitebark pine seedling. Insolation mortality of whitebark pine was higher on mineral, litter, and burned seedbeds on nonshaded plots when compared to 25 and 50 percent shaded plots in a germination test in southwestern Montana, U.S.A. (McCaughey 1990).

Blister Rust—The introduced disease, blister rust (*Cronartium ribicola*), poses the most serious threat to

Table 2—Percent germination¹ of 1987 sown whitebark pine seed (buried 2 to 4 cm) as affected by shade cover and seedbed condition for each of the first 3 years following sowing and the 3-year total. Data collected from a clearcut at 2,530 m elevation in southwestern Montana, U.S.A.

Factor	Factor level	Emergence			
		First year	Second year	Third year	Three-year total
		----- Percent -----			
Shade cover (percent)	0	10	39	5	² 47 (a)
	25	13	51	14	61 (a)
	50	12	46	15	60 (a)
Seedbed condition	Mineral	13	40	7	51 (a)
	Litter	9	50	15	60 (a)

¹Percent germination for each year is based on the number of seeds that had not previously emerged.

²Similar and dissimilar letters in parentheses for a factor represent statistically nonsignificant and significant differences respectively.

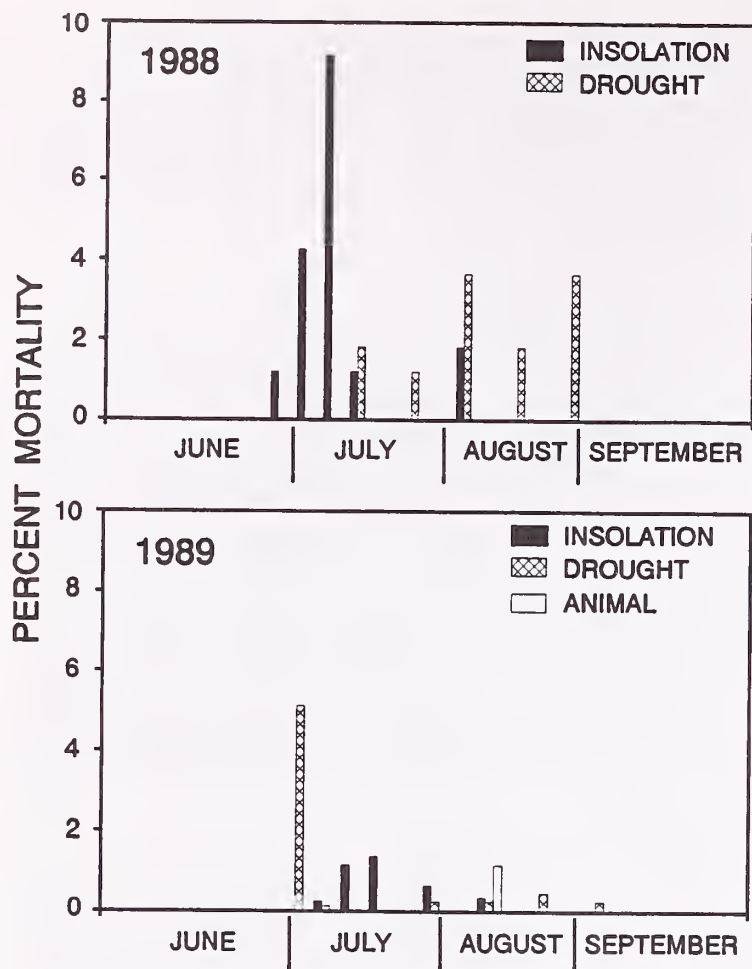


Figure 4—Percent first-year mortality of whitebark pine seedlings by causal agent over time for 1987 and 1988 sown seeds. Data collected from a clear-cut at 2,530 m elevation in southwestern Montana, U.S.A.

the survival of whitebark pine in parts of its distributional range. Blister rust was brought to western North America in 1910 on a boatload of blister rust-infected eastern white pine (*Pinus strobus* L.). Whitebark pine is the most susceptible to blister rust infection of 14 white pines rated by Bingham (1972). Blister rust causes extensive damage and mortality in whitebark pine stands in moist mountain regions in northwestern Montana, northern Idaho, and the Washington Cascades in the United States (Arno 1986). Damage is light where environmental conditions are somewhat dry and cold, and there is a decrease in low-elevation sources of inoculum (Hoff and Hagle 1990).

Blister rust-infected trees may live for several years before mortality occurs; during that time cone production is reduced due to loss of upper crowns. Mortality from rust favors succession toward dominance by whitebark pine's shade-tolerant associates thus reducing site potential for whitebark pine regeneration and survival (Arno 1986; Arno and Hoff 1989; McCaughey and Schmidt 1990).

The degree of blister rust infection on whitebark pine decreases southward for all parts of its range (Hoff and Hagle 1990; Keane and others 1990). A major population of whitebark pine exists in the Yellowstone ecosystem of southwestern Montana and northwestern Wyoming, U.S.A.

The Yellowstone environment is poorly suited to blister rust infection because it has a cool, dry climate that is only marginally suitable for blister rust teliospore germination (Krebill 1971).

Mountain Pine Beetle—Mountain pine beetle is the most damaging insect in mature stands of whitebark pine (Arno and Hoff 1989; McCaughey and Schmidt 1990). Large numbers of whitebark pine are killed by mountain pine beetle when epidemics spread into whitebark pine stands from the lower elevation lodgepole pine zone. These epidemics, like blister rust, create conditions where succession progresses toward dominance by shade-tolerant conifers such as subalpine fir and Engelmann spruce (Arno 1986).

Fire Suppression—Whitebark pine is seral to subalpine fir and other conifers, and periodic fires have helped to perpetuate the pine (Arno 1986). Past fire intervals in whitebark pine stands ranged from 50 to 300 years or more depending on site conditions (Arno 1980). Fires occur in whitebark pine stands only under severe burning conditions and are typically non-stand replacing. Fires sweep across large areas of forest reducing competition from shade-tolerant conifers (Arno 1976). Nearly 90 years of fire suppression have reduced the annual acreage of whitebark pine forests being burned, creating conditions where shade-tolerant species have taken over what were once seral whitebark pine stands.

Severe fire conditions are being created by increased mortality and the buildup of fuels in whitebark pine stands due to mountain pine beetle and blister rust epidemics. Stand replacement fires will be the result of this unnatural fuel loading and will eliminate large cone-producing stands of whitebark pine.

VEGETATIVE REPRODUCTION

Whitebark pine can reproduce vegetatively through layering of lower branches along the ground surface. In the Mission Range of western Montana vegetative reproduction was observed from layering of shrublike (krummholz) whitebark pine (Arno 1981; Arno and Hoff 1989). Although layering is possible, the vast majority of reproduction is from seeds.

SUMMARY

Regeneration processes are similar for whitebark pine and the other stone pines of the world. The initiation, development, and maturation of cones and seeds for whitebark pine are characteristic of five-needle pines in general with seasonal timing of these processes varying between species. The entire process from cone initiation to cone and seed maturity takes about 24 months. Cone and seed development are most affected by variations in climatic conditions during periods of reproductive bud formation, pollination, and growth and development. Several insects and diseases reduce survival of cones and seeds of whitebark pine.

Regeneration of whitebark pine depends almost exclusively on the seed selection, dispersal, and caching habits

of the Clark's nutcracker. Other stone pines of the world have similar mutualistic relationships with bird species for seed dispersal.

Whitebark pine seeds are cached by Clark's nutcrackers on a variety of sites ranging from forest litter to cracks and fissures in rocks. The majority of regeneration occurs on south or west aspects. Seed storage in south-aspect windblown sites ensures that some caches are snow free in winter and spring for nutcracker retrieval. Regeneration densities are highest on north aspects even though fewer seeds are cached there because of favorable microsite conditions such as moisture and insolation protection.

Germination of whitebark pine begins about mid-June and continues through early September in the first year following caching. Delayed germination occurs for up to 3 or 4 years after caching. Total germination over a 3-year period is highest on litter seedbeds that have 50 percent shade cover, while germination is lower on mineral and nonshaded seedbeds (McCaughy, in press b). Dormancy of whitebark pine seed is caused by embryo underdevelopment, physiological embryo dormancy, and imperviousness of the seed coat and female gametophyte tissue to oxygen and water uptake.

Factors limiting survival of whitebark pine seedlings are microsite, biotic, disease, insects, and fire. Insolation and drought are microsite-associated factors that cause seedling mortality. Animals such as pocket gophers bury, uproot, or nip off young seedlings, and chipmunks uproot and consume whole seedlings. Deer mice and southern red-backed voles and other small mammals consume seed before they germinate. Blister rust causes mortality or extensive damage of the cone-bearing portions of the tree. Whitebark pine is killed by the mountain pine beetle when epidemics spread into whitebark pine stands from the lower elevation lodgepole pine zone. Fire suppression creates conditions where shade-tolerant species such as Engelmann spruce and subalpine fir, normally killed by light underburns, take over through succession what were once seral whitebark pine stands. Severe fire conditions are being created by the buildup of fuels in whitebark pine stands due to increased mortality.

We are beginning to piece together the puzzle of the regeneration process of whitebark pine. Survival of wildlife species such as the grizzly is threatened due to a reduction or loss of localized populations of whitebark pine caused by global climate change, introduced disease, insects, and succession from fire exclusion. Future research should define microsite and biotic factors influencing germination and long-term survival of seedlings. Information on regeneration processes from other stone pine species from around the world is helping identify key areas for research on whitebark pine. For example, little information is available on the elevational distribution of whitebark and which habitats are best suited for regeneration. Cembra pine (*Pinus cembra*) grows in the Swiss Alps from valley bottoms to timberline when management actions reduce intertree competition. Whitebark pine management will improve from increased knowledge of regeneration processes of all the stone pines.

REFERENCES

- Arno, S. F. 1976. The historical role of fire on the Bitterroot National Forest. Res. Pap. INT-187. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 30 p.
- Arno, S. F. 1980. Forest fire history in the Northern Rockies. *Journal of Forestry*. 78(8): 460-465.
- Arno, S. F. 1981. [Unpublished observations]. Missoula, MT: U.S. Department of Agriculture, Forest Service, Intermountain Fire Sciences Laboratory.
- Arno, S. F. 1986. Whitebark pine cone crops - a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-94.
- Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.
- Bartos, D. L.; Gibson, K. E. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 171-178.
- Bingham, R. T. 1972. Taxonomy, crossability, and relative blister rust resistance of 5-needled white pines. In: *Biology of rust resistance in forest trees: proceedings of a NATO-IUFRO advance study institute*; 1969 August 17-24; Moscow, ID. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture: 271-280.
- Bock, W. J.; Balda, R. P.; Vander Wall, S. B. 1973. Morphology of the sublingual pouch and tongue musculature in Clark's nutcracker. *Auk*. 90: 491-519.
- Craighead, J. J.; Sumner, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. *Wildlands Inst. Monogr.* 1. Missoula, MT: University of Montana. 279 p.
- Dewey, Jerald E. 1989. [Personal communication to Dale Bartos of Intermountain Research Station, Logan, UT]. March 27. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region.
- Edwards, D. G. W. 1990. Cone prediction, collection and processing. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 78-102.
- Eggers, D. E. 1986. Management of whitebark pine as potential grizzly bear habitat. In: Contreras, G. P.; Evans, K. E., comps. *Proceedings—grizzly bear habitat symposium*; 1985 April 30-May 2; Missoula, MT. Gen. Tech. Rep. INT-207. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 170-175.

- Furnier, G.; Knowles, P.; Clyde, M.; Dancik, B. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. *Evolution*. 41: 607-612.
- Harlow, W. M. 1931. The identification of the pines of the United States, native and introduced, by needle structure. Tech. Publ. 32. Syracuse, NY: New York State College of Forestry. 21 p.
- Hoff, R. J. 1992. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Moscow, ID.
- Hoff, R. J.; Hagle, S. 1990. Diseases of whitebark pine with special emphasis on white pine blister rust. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 179-190.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Jacobs, J. S. 1989. Temperature and light effects on seedling performance of *Pinus albicaulis*. Bozeman, MT: Montana State University. 39 p. Thesis.
- Jacobs, J.; Weaver, T. 1990a. Effects of temperature and temperature preconditioning on seedling performance of whitebark pine. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 134-139.
- Jacobs, J.; Weaver, T. 1990b. Occurrence of multiple stems in whitebark pine. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 156-159.
- Keane, R. E.; Arno, S. F.; Brown, J. K.; Tomback, D. F. 1990. Simulating disturbances and conifer succession in whitebark pine forests. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 274-288.
- Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. In: International Conference on Bear Research and Management. Madison, WI: International Bears Association. 5: 166-173.
- Knight, R. R.; Blanchard, B. M.; Mattson, D. J. 1987. Yellowstone grizzly bear investigation: report of the interagency study team, 1987. Bozeman, MT: U.S. Department of the Interior, National Park Service. 80 p.
- Krebill, R. G. 1971. Conditions for teliospore germination in Yellowstone National Park environment. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Krugman, S. L.; Jenkinson, J. L. 1974. *Pinus* L. pine. In: Schopmeyer, C. S., ed. Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: 598-638.
- Landis, T. D.; Tinus, R. W.; McDonald, S. E.; Barnett, J. P. 1990. The biological component: nursery pests and mycorrhizae. Vol. 5. The container tree nursery manual. Agric. Handb. 674. Washington, DC: U.S. Department of Agriculture, Forest Service. 171 p.
- Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Sixth North American forest biology workshop proceedings; 1980 August; Edmonton, AB. Edmonton, AB: University of Alberta: 14-48.
- Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. *Canadian Journal of Forest Research*. 12(2): 391-402.
- Lanner, R. M.; Vander Wall, S. B. 1980. Dispersal of limber pine seed by Clark's nutcracker. *Journal of Forestry*. 78(10): 637-639.
- Leadem, C. L. 1985. Seed dormancy in three *Pinus* species of the Inland Mountain West. In: Schmidt, Wyman C., comp. Proceedings—future forests of the Mountain West: a stand culture symposium; 1986 September 29-October 3; Missoula, MT. Gen. Tech. Rep. INT-243. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 117-124.
- Linhart, Y.; Tomback, D. F. 1985. Seed dispersal by nutcrackers causes multi-trunk growth form in pines. *Oecologia*. 67: 107-110.
- McCaughey, W. W. 1990. Biotic and microsite factors affecting *Pinus albicaulis* establishment and survival. Bozeman, MT: Montana State University. 78 p. Dissertation.
- McCaughey, W. W. 1988. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT.
- McCaughey, W. W. 1992. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT.
- McCaughey, W. W. [In press a]. Seasonal maturation of whitebark pine seed in the Greater Yellowstone ecosystem. In: Schullery, Paul; Despain, Don, comps. Proceedings of the 1st biennial scientific conference on the Greater Yellowstone Ecosystem—plants and their environments; 1991 September 16-17; Mammoth Hot Springs, Yellowstone National Park, WY. Tech. Rep. USDI National Park Service.
- McCaughey, W. W. [In press b]. Delayed germination and seedling emergence of *Pinus albicaulis* in a high elevation clearcut in Montana, U.S.A. In: Edwards, D. G., comp. Proceedings—symposium: seed dormancy and barriers to germination; 1991 April 23-26; IUFRO

- project group P2.04-00 meeting on seed problems; Victoria, BC. Victoria, BC: Forestry Canada.
- McCaughey, W. W.; Arno, S. F.; Tomback, D. F. 1990. Unpublished personal observations from Henderson Mountain near Cooke City, MT, U.S.A.. On file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Bozeman, MT.
- McCaughey, W. W.; Schmidt, W. C. 1990. Autecology of whitebark pine. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 85-96.
- Mirov, N. T. 1946. Viability of pine seed after prolonged cold storage. *Journal of Forestry*. 44(3): 193-195.
- Mirov, N. T. 1967. The genus *Pinus*. New York: The Ronald Press. 602 p.
- Morgan, Penny; Bunting, Stephen C. 1990. Fire effects in whitebark pine forests. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 166-170.
- Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.
- Pitel, J. A. 1981. Improved germination of whitebark pine (*Pinus albicaulis* Engelm.) seeds. Chalk River, ON: Canadian Forestry Service, Petawawa National Forestry Institute; unpublished report. 5 p.
- Pitel, J. A.; Wang, B. S. P. 1980. A preliminary study of dormancy in *Pinus albicaulis* seeds. *Bi-Monthly Research Notes*. 36(1): 4-5.
- Pitel, J. A.; Wang, B. S. P. 1990. Physical and chemical treatments to improve germination of whitebark pine seeds. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 130-133.
- Reinhart, D. P. 1990. [Personal communication]. August. Bozeman, MT: U.S. Department of the Interior; Montana State University, Interagency Grizzly Bear Project.
- Reinhart, D. P.; Mattson, D. J. 1990. Red squirrels in the whitebark zone. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 256-263.
- Schmidt, W. C.; Lotan, J. E. 1980. Phenology of common forest flora of the Northern Rockies—1928 to 1937. Res. Pap. INT-259. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 20 p.
- Schmidt, W. C.; McDonald, K. J., comps. 1990. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 386 p.
- Schubert, G. H. 1954. Viability of various coniferous seeds after cold storage. *Journal of Forestry*. 52: 446-447.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. *Ecological Monographs*. 38: 31-63.
- Steele, R.; Cooper, S. V.; Ondov, D. M.; Roberts, D. W.; Pfister, R. D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.
- Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. *Living Bird*. 16(1977): 123-160.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology*. 51(2): 451-467.
- Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Nitecki, M. H., ed. *Coevolution*. Chicago and London: University of Chicago Press: 179-223.
- Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. *Madroño*. 33(2): 100-110.
- Tomback, D. F. 1992. Unpublished data on file at: Department of Biology, University of Colorado at Denver, Denver, CO.
- Tomback, D. F.; Hoffmann, L. A.; Sund, S. K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-129.
- Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs*. 47: 89-111.
- Weaver, T.; Jacobs, J. 1990. Occurrence of multiple stems in whitebark pine. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 156-159.

JAPANESE STONE PINE CONE PRODUCTION ESTIMATED FROM CONE SCARS, MOUNT KISOKOMAGATAKE, CENTRAL JAPANESE ALPS

Ikuko Nakashinden

Abstract—The past cone production of the Japanese stone pine (*Pinus pumila*) on Mount Kisokomagatake was reconstructed from cone scars. The main cone production was by larger individuals in the lower part of the scrub zone; it was greater than that in the upper part where growth and crop are controlled mainly by strong winter winds and snow.

The Japanese stone pine (*Pinus pumila* Regal) is a genetic dwarf pine distributed over the eastern part of Siberia and China, the northern part of Korea, and Japan. In Japan, most of its habitats are located on high mountains. The climax scrub zone is formed above the timberline of subalpine coniferous forests. At the southern margin of its range (Chubu District) the scrub zone occupies the altitudinal zone from 1,961 to 3,192 m (Yanagimachi and Ohmori 1991).

The Japanese stone pine propagates in two different ways: one by the expansion of shoots and the other by seeds. The latter is the most important for spatial expansion (Okitsu 1990). Seeds are dispersed by seed-storing corvids (*Nucifraga caryocatactes*) (Hayashida 1989; Tomback 1990). Studies concerning pine cone production have begun recently. Okitsu and Mizoguchi (1990, 1991) evaluated pine cone productivity based on the individual growth sizes and scrub sizes. In addition, studies of the relationship between environment of the habitats and cone production have commenced (Nakashinden 1990). These studies are limited to 1 year's cone production data. It is notable that past cone production can be estimated from cone scars. This was done on whitebark pine (*Pinus albicaulis*) in the United States (Morgan and Bunting 1992; Weaver and Forcella 1986). Saito and others (1989) reported that cone scars are also recognizable in the Japanese stone pine in Hokkaido, but little information about it was given in their report.

This author developed the method to reveal the yearly change in cone production for the Japanese stone pine and succeeded in reconstructing pine cone production over the past 15 years (Nakashinden 1991). Using this cone scar method, chronological pine cone production of the Japanese stone pine is described and the relationship to the environment of its habitats is examined.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Ikuko Nakashinden is Graduate Student, Department of Geography, University of Tokyo, Bunkyo-ku, Tokyo 113, Japan.

STUDY AREA AND METHODS

The study area is located on Mount Kisokomagatake, whose summit is 2,956 m, in the Central Japanese Alps, in Chubu District (fig. 1). This location is one of the southernmost parts of the Japanese stone pine distribution.

The habitats examined are located on the mountain slopes between 2,600 and 2,950 m elevation, including the summits of Mount Kisokomagatake and Mount Chausudake (2,652 m). In this altitudinal zone, the Japanese stone pine is dominant, forming its own vegetation zone above the subalpine forest of *Abies veitchii*, *Tsuga diversifolia*, *Betula ermanii*, and *Alnus maximowiczii*.

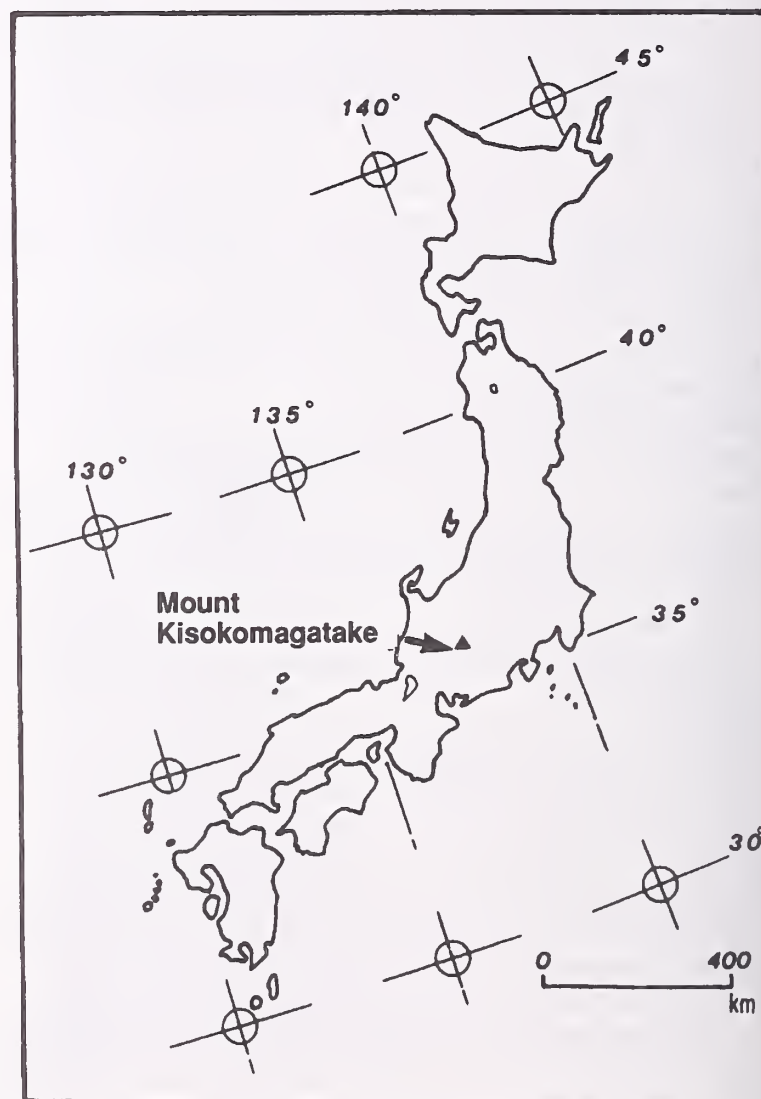


Figure 1—Location of Mount Kisokomagatake.

Pine Cone Scars

The positions of pine cones of the Japanese stone pine are restricted to the first nodes of the annual shoots. They mature in the second year after fruiting. In September, nutcrackers harvest cones of the Japanese stone pine as a food source. When the pine cone is picked, a scar of the cone remains on the stem (Nakashinden 1991; Saito and others 1989). Each scar represents one cone. From these scars, the number of pine cones can be calculated. The production can be determined from the location of the nodes on the stems. This cone scar method was used on whitebark pine in the United States, and the scars could be measured for 6 to 8 years (Weaver and Forcella 1986), or 6 to 12 years (Morgan and Bunting 1992). For the Japanese stone pine, the scars could be counted for 15 to 20 years (Nakashinden 1991).

Using this method, 32 plots (1 m²) at different altitudes from 2,600 m near the forest line to 2,950 m near the summit were investigated. Ten stems in each plot were selected for counting pine cone scars and for the measurement of individual stem growth for the 15 years preceding 1990.

Distribution, Geomorphology, and Snow

Using color aerial photographs and field observation, the Japanese stone pine scrubs in the study area were delineated and mapped. Some topographical maps were made during the field survey in order to examine the microscale landform beneath the scrubs. The snow melting status and snow melting period near the summit of Mount Kisokomagatake was observed and recorded on photographs in each spring season from 1989 to 1991.

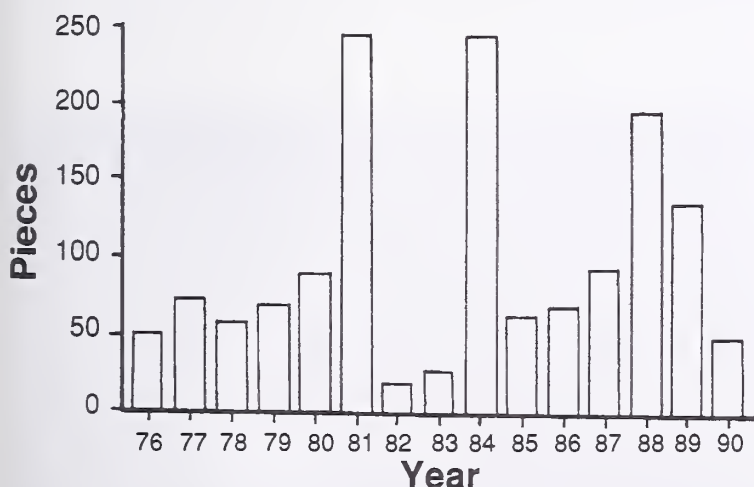


Figure 2—Annual cone crops of Japanese stone pine (1976-90). Cone crops were reconstructed from cone scars on the stems. Total number from 32 plots is shown for each year.

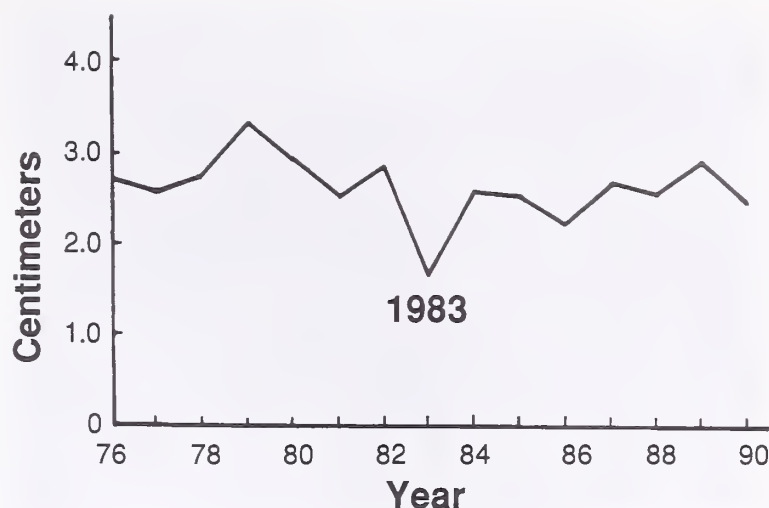


Figure 3—Mean annual stem elongation of Japanese stone pine (1976-90). Ten stems each in 32 plots were measured.

CONE PRODUCTION OVER 15 YEARS

The past 15 years of pine cone production was reconstructed on the study area (fig. 2). Mast years were recognized in 1981, 1984, 1988, and 1989, showing a 3- or 4-year periodicity of cone production. The lowest production during the past 15 years occurred in 1982 and 1983. In 1983, the annual shoot length was also the lowest during the 15-year period (fig. 3). The year 1983 is judged to be one of the worst years for both cone crop and growth.

On the individual plots, both mast and fail years occurred regardless of their environmental differences. For the mast years, 68 percent of the 32 plots showed high production in 1981, and in 1984 it was 65 percent. For the fail years, 59 percent of the plots failed in cone production in 1982, and in 1983 it was 63 percent. These occurrences were dependent on the climate and not on the growth forms or the location of scrubs.

DISTRIBUTION PATTERNS BY ALTITUDE

On Mount Kisokomagatake, the Japanese stone pine scrubs dominate and form a vertical zone above the subalpine forest at an elevation between 2,600 and 2,950 m. However, the distribution patterns were characterized by the altitude. On the upper part from 2,850 up to 2,950 m, near the summit of Mount Kisokomagatake, the distribution pattern of the scrubs shows a stripe pattern (fig. 4).

The scrubs are fragmented by huge granite rocks, tors, stone bank terraces, trails, and alpine plant communities such as *Arctous alpinus* var. *japonicus*, *Diapensia lapponia* var. *obovata*, *Oxytropis japonica* Maxim, *Leontopodium shinanense* Kitam, *Gentiana algida* Pall., and *Loiseleuria procumbens* Desv. The lower part between 2,850 and 2,600 m, near the boundary to the subalpine forest shows an extensively spreading scrub, covering the slopes entirely from the ridges down to the forest limit (fig. 5).



Figure 4—Distribution pattern of Japanese stone pine scrubs in the upper part of the Mount Kisokomagatake study area. Distribution is fragmented by huge rocks, tors, stone bank terraces, trails, and alpine plant communities.

GROWTH FORM AND CONE PRODUCTION RELATED TO ALTITUDE

Growth form and pine cone production are different between the upper and the lower part of the Japanese stone pine scrub zone (table 1). The mean scrub height, stem length, and diameter at the stem base in the lower part are almost twice as large as those in the upper part. The mean pine cone production per stem is 1.5 times more than in the upper part. Although the number of stems per square meter in the upper part was twice that of the lower part, the Japanese stone pine scrubs in the lower part were larger in size and produced more cones than the scrubs in the upper part.



Figure 5—Distribution pattern of Japanese stone pine scrubs in the lower part of the Mount Kisokomagatake study area. They spread extensively and cover the slopes entirely from the ridges down to the forest line.

DISCUSSION AND CONCLUSIONS

On Mount Kisokomagatake, the mean summer temperature (July and August) was 10 to 12 °C at 2,600 m (Koizumi 1974) and 10 °C (Nakashinden 1990, unpublished) at 2,850 m. Concerning the lower parts of the Japanese stone pine scrub zone, the thermal conditions indicate that the Japanese stone pine scrub zone is included in the thermal subalpine zone (Yanagimachi and Ohomori 1991). There, the Japanese stone pine scrubs are considered to grow and produce cones at the same rates as in the subalpine zone.

The scrubs in the upper part are explained by other environmental factors unfavorable for growth and cone production. In the Japanese stone pine scrub zone, the scrub height is related to winter wind strength and snow depth of their habitats (Okitsu 1987). In high-mountain areas, the Japanese stone pine needs to be protected by snowpack to evade physical damages or dehydration caused by strong winds. Short scrub height indicates strong winds and shallow snow cover at the habitats during the winter season, while tall scrub height indicates moderate winds and heavy snowpack.

On Mount Kisokomagatake, the depth of snow varies from 10 cm to 3 m according to landforms and wind velocity (Koizumi 1974). Especially around the summit, most of the snow is blown away from the windward slope by strong westerly winds (fig. 6). Snow accumulates on the leeward side of the ridges or rocks. On the windward slope, characterized by shallow snow cover, the Japanese stone pine grow close to the ground, thus protecting themselves from strong winds (fig. 7). Therefore, vertical growth of the Japanese stone pine scrubs is disturbed by winter winds.

Variation in snow depth caused differences in the length of the snow melting period. According to 3 years' observation by this author, snow on the Japanese stone pine scrubs located on windward slopes started to melt

Table 1—The growth and pine cone production in each part of the distribution zone viewed from different altitude of quadrats. The boundary of the upper and the lower part is 2,850 m

Cone production and growth	Upper part	Lower part
Cone production (pieces)	4.1	6.4
Mean scrub height (cm)	36.2	89.2
Mean stem length (cm)	92.0	180.0
Mean diameter at stem base (cm)	2.2	4.2
Mean annual stem elongation (cm)	2.4	3.0
Number of stems/m ²	38.5	20.0

¹The values indicate the means of 20 plots for the upper part and 12 plots for the lower part.



Figure 6—Mount Kisokomagatake summit in early spring (1991). Snow depth varies according to wind velocities and topography. The western-most part (left) where snow cover was thin due to strong westerly winds shows earliest snow melt in spring.

at the end of April. On the leeward slopes, the scrubs became completely free of snow by the middle of June. On the slopes where snow remains until the end of July, the Japanese stone pine is replaced by alpine snowbed vegetation. On the other hand, shallow snow cover causes early snow melt and solifluction is very common. Solifluction forms stone banked terraces and cuts off the roots of young plants. For this reason, the Japanese stone pine scrubs in the upper part are not able to cover all the slopes and thus show a fragmented distribution pattern.

These severe environmental conditions are not favorable for growth or cone production of the Japanese stone pine. The main cone production is performed by large and



Figure 7—Creeping Japanese stone pine in the upper part of the study area. The scrubs' height is 10-15 cm. The stem has branches flagged toward the leeward side. The plot shows one of the lowest cone productions (only one cone for 10 stems) during these 15 years.

tall scrubs at the lower elevations where winter winds are moderate and snow is evenly distributed.

ACKNOWLEDGMENTS

I thank Professor Dr. F.-K. Holtmeier, Dr. Wyman C. Schmidt, and Dr. W. Schönenberger for their invitation to attend the workshop. I thank Dr. Professor Hiroo Ohmori and Dr. Takeei Koizumi for their valuable advice in carrying out this study. My thanks also go to Dr. Tad Weaver and Dr. Penelope Morgan for providing me with information about cone scar methods on whitebark pine. Dr. Mitsuhiro Hayashida offered me valuable information in preparation for the workshop. I am grateful to all my colleagues in the Geography Department of Tokyo Gakugei University, who enthusiastically helped me in my field research on Mount Kisokomagatake. I thank Mr. Wataru, Mrs. Joyce Mukai, and Mr. Garrett Vance who checked my manuscript. And I thank Dr. Miki Kobayashi who always encourages me to keep studying *Pinus pumila*.

REFERENCES

- Hayashida, M. 1989. Seed dispersal and regeneration patterns of *Pinus parviflora* var. *pentaphylla* on Mt. Apoi in Hokkaido. Research Bulletins of the College Experimental Forests, Faculty of Agriculture, Hokkaido University. 46-1: 177-190.
- Kajimoto, T. 1989. Above-ground biomass and litterfall of *Pinus pumila* scrubs growing on the Kiso Mountain Range in central Japan. Ecological Research. 4: 55-69.
- Koizumi, T. 1974. Landschaftsökologische Untersuchungen in der Alpine Stufe des Kisokomagatake in der Japanischen Zentralalpen mit Besonderer Berücksichtigung der Vegeta Strukturbodens. Japanese Journal of Ecology. 24(2): 78-91.
- Mizoguchi, T.; Okitsu, S. 1987. Cone production of *Pinus pumila* Regal in high mountains in central Japan with special attention to basal diameter and annual elongation on it. In: Transactions of the 98th annual meeting of the Japanese Forestry Society; 1987 April; Kyushu: 363-364.
- Morgan, P.; Bunting, S. C. 1992. Technical note: cone crops of whitebark pine. Western Journal of Applied Forestry. 7(3): 71-73.
- Nakashinden, I. 1990. Pine cone production of *Pinus pumila* and their environment in Mt. Kisokomagatake, Nagano prefecture. In: Transactions of the 38th autumnal meeting of the Association of Japanese Geographers; 1990 September; Niigata: 104-105.
- Nakashinden, I. 1991. Pine cone production of *Pinus pumila* reconstructed from pine cone scars. In: Transactions of the 39th spring meeting of the Association of Japanese Geographers; 1991 April; Tokyo: 28-29.
- Okitsu, S. 1984b. Comparative studies on the Japanese alpine zone, with special reference to the ecology of *Pinus pumila* thickets. Geographical Review of Japan. 57(11): 170-172.
- Okitsu, S. 1987. *Pinus pumila* zone. In: Ito, K., comp. Vegetation of Hokkaido. Hokkaido, Japan: Hokkaido University Press: 129-167.

- Okitsu, S.; Ito, K. 1983. Dynamic ecology of the *Pinus pumila* community of Mts. Taisetsu, Hokkaido, Japan. The Environmental Science, Hokkaido University. 6(1): 151-184.
- Okitsu, S.; Mizoguchi, T. 1986. Cone production of *Pinus pumila* community on Mt. Senjo, Akaishi Range, central Japan. In: Transactions of the 97th annual meeting of the Japanese Forestry Society; 1986 April; Utsunomiya: 343-344.
- Okitsu, S.; Mizoguchi T. 1990. Relation between cone production and stem diameter and stem elongation of *Pinus pumila* of Japanese high mountains. Japanese Journal of Ecology. 40(2): 49-55.
- Okitsu, S.; Mizoguchi, T. 1991. Cone production of *Pinus pumila* scrubs. Japanese Journal of Ecology. 41(2): 101-107.
- Saito, S.; Kawabe, M.; Nakaoka, T. 1989. On the forest vegetation of Mt. Upepesanke, Tokachi, Hokkaido. (1): On a thicket of *Pinus pumila* at the ridge of 1610 m. Bulletin of the Higashi Taisetsu Museum of Natural History. 11: 23-34.
- Saito, S.; Kawabe, M. 1990. On the forest vegetation of Mt. Higashi-Nupukaushinupuri, Tokachi, Hokkaido. (2): On two thickets of *Pinus pumila*. Bulletin of the Higashi Taisetsu Museum of Natural History. 12: 17-29.
- Tomback, D.; Linhart, Y. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219.
- Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, R. C., comp. Proceedings—conifer tree seed in the Inland Mountain West; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.
- Yanagimachi, O.; Ohmori, H. 1991. Ecological status of *Pinus pumila* scrub and the lower boundary of the Japanese alpine zone. Arctic and Alpine Research. 23(4): 242-435.

EFFECTS OF SEED DISPERSAL BY CLARK'S NUTCRACKER ON EARLY POSTFIRE REGENERATION OF WHITEBARK PINE

Diana F. Tomback

Abstract—Clark's nutcrackers (*Nucifraga columbiana*) bury whitebark pine (*Pinus albicaulis*) seeds in recently burned terrain. Studies of early postfire whitebark pine regeneration in the Northern Rocky Mountains indicate that seed dispersal by nutcrackers (1) may be more effective than seed dispersal by wind in restocking large burns, particularly when the seed source is unfavorably positioned with respect to prevailing winds, and (2) produces a negative exponential distribution when whitebark pine regeneration density is plotted vs. distance from the seed source. Whitebark pine seeds can remain dormant for one or more years after dispersal, which results in continuity of regeneration over time.

Fire is an ecologically important, recurring event in most western North American montane forests, including those regions where whitebark pine (*Pinus albicaulis*) is found. Fire-prone areas are those with fuel accumulation, dry, windy weather, and periods of frequent lightning storms. In the Northern Rocky Mountains, fire burns whitebark pine communities every 50 to 300 years (Arno 1980; Arno and Petersen 1983; Romme 1980). Stand-replacing fires result in the renewal of successional whitebark pine communities, and underburns kill the less fire-resistant subalpine fir (*Abies lasiocarpa*). In the absence of fire in these communities, whitebark pine is often replaced by more shade-tolerant conifers, particularly subalpine fir (Arno 1986; Arno and Hoff 1989).

Studies of early postfire regeneration, defined here as the first 3 decades after fire, provide information on the dynamics of seed dispersal and seedling establishment for whitebark pine and associated conifers. Clark's nutcrackers (*Nucifraga columbiana*) are the principal dispersal agents for whitebark pine seeds, in contrast to other conifers whose seeds are wind-dispersed. Nutcrackers bury caches of one to 15 or more ripe whitebark pine seeds at distances from parent trees of a few meters to 22 km (Hutchins and Lanner 1982; Tomback 1978, 1982; Vander Wall and Balda 1977; see review in Tomback and Linhart 1990). In contrast, most wind-dispersed seeds land only within about 120 m of parent trees (McCaughy and others

1986), although updrafts and storms may disperse some seeds over longer distances. Often, the regeneration from nutcracker caches is in the form of whitebark pine seedling clusters (for example see Tomback 1982, 1986; Tomback and others 1990, 1993), which may result in mature multi-genet tree clusters (see Tomback and Schuster, these proceedings, and references therein). In this paper I summarize the results of recent studies that compare patterns of early postfire regeneration of the bird-dispersed whitebark pine and its wind-dispersed forest associates.

REGENERATION IN WESTERN MONTANA

Studies of two large, severe subalpine burns in western Montana (Bitterroot National Forest, Ravalli County) illustrate how seed dispersal by nutcrackers affects patterns of early postfire regeneration of whitebark pine and associated conifers. These two study areas were selected for similarities in topography, severity of burn, forest types, and time elapsed since fire. In this region of western Montana, whitebark pine is abundant between about 2,290 and 2,620 m elevation (Arno and Hoff 1989; Pfister and others 1977), and the prevailing winds in late summer and fall are from the west and southwest (Finklin 1983). The prefire forest in both study areas was a seral whitebark pine community. Reported results from these studies are summarized here from Tomback and others (1990, 1993).

The Sleeping Child Burn resulted from a wildfire in 1961 that burned about 11,350 ha of forest on the west slope of the Sapphire Range. The nearest whitebark pine seed source is mature forest above 2,250 m on the eastern edge of the burn. Subalpine fir, Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*) are also present in this upper seed source as well as around the lower perimeters of the burn. Because the prevailing winds are from the west, wind-dispersed seeds are irregularly dispersed into the eastern portion of the burn from the upper seed source.

In 1987, we established a 3.6-km-long transect along an eastwest trending ridge, running from the seed source into the northern center of the burn (fig. 2 in Tomback and others 1990). Elevation along the ridge decreases from about 2,480 to 2,150 m with increasing distance from the eastern edge of the burn. Every 150 m along the transect we established parallel quadrats, each 50 m long, on the ridgetop, north, and south aspects of the ridge for

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Diana F. Tomback is Associate Professor of Ecology, Department of Biology and Center for Environmental Sciences, University of Colorado at Denver, Denver, CO 80217-3364.

a total of 63 quadrats. Quadrat widths varied in preset increments from 1.25 to 15 m, with respect to local densities of whitebark pine. For each quadrat we recorded all conifer regeneration.

The Saddle Mountain Burn resulted from a wildfire in 1960 that spread over 1,240 ha of forest in the Bitterroot Mountains west of Lost Trail Pass. Running northeast to southwest in the longest dimension, the burned area ranges in elevation from about 1,950 to 2,475 m. On the southwest edge of the burn above 2,275 m, the whitebark pine seed source is positioned so that the burned area is leeward with respect to prevailing winds. Subalpine fir, Engelmann spruce, and lodgepole pine also occur in this upper seed source and, with Douglas-fir (*Pseudotsuga menziesii*), around the lower perimeters of the burn.

In 1988 we established two parallel 3.2-km-long transects beginning at the seed source and heading northeast through the southern portion of the burn (fig. 4 in Tomback and others 1990). We set up 41 quadrats and recorded all regeneration according to the general methodology outlined earlier for the Sleeping Child Burn (for details of methodology, see Tomback and others 1990, 1993).

Mean whitebark pine regeneration density sampled per quadrat in the Sleeping Child Burn was much greater than that of its shade-tolerant competitors, subalpine fir

Table 1—Mean density and standard deviation (S.D.) per quadrat for conifer¹ regeneration 26 years and 28 years after fire in the Sleeping Child and Saddle Mountain Burns, respectively. Based on Tomback and others (1990)

	Regeneration sites per m ²				
	PIAL	ABLA	PIEN	PICO	PSME
Sleeping Child					
\bar{x}	0.070	0.008	0.004	0.039	—
S.D.	.104	.014	.009	.066	—
Saddle Mountain					
\bar{x}	.044	.046	.030	.323	0.019
S.D.	.050	.068	.044	.355	.032

¹PIAL = whitebark pine, ABLA = subalpine fir, PIEN = Engelmann spruce, PSME = Douglas-fir.

and Engelmann spruce, and greater than the shade-intolerant lodgepole pine as well (table 1). Scatterplots of quadrat densities vs. distance from the upper seed source revealed interesting differences in regeneration patterns among the conifers (fig. 1). The scatterplot for whitebark pine was a negative exponential curve, with the highest densities near the seed source and a long tail indicating

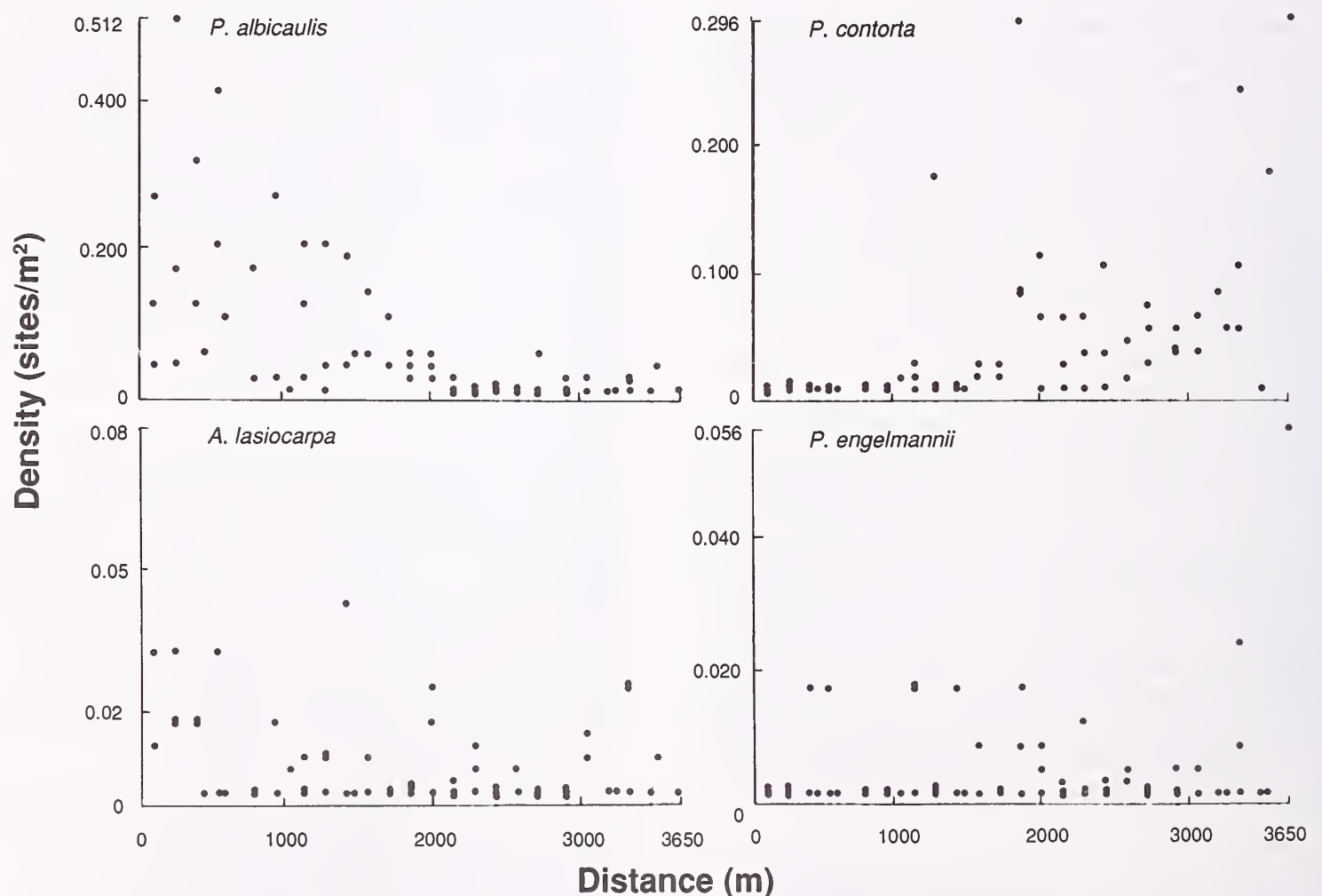


Figure 1—Scatterplots of regeneration density per quadrat versus distance from the whitebark pine seed source for four conifer species in the Sleeping Child Burn. Clockwise from left: whitebark pine, lodgepole pine, Engelmann spruce, subalpine fir. From Tomback and others (1990).

some regeneration beyond 3.6 km. Quadrat density vs. distance in subalpine fir showed a negative linear relationship, indicating that the primary seed source for this species was also the upper, unburned forest. In contrast, the scatterplot for Engelmann spruce was nearly flat, with the highest values at the lower end of the transect, suggesting that seeds may be blown into the ridge area from both the higher and lower seed sources. For lodgepole pine, densities increased with distance from the upper, unburned forest (are higher at lower elevations). Before the fire, the lower and middle elevations of this area were dominated by lodgepole pine, and thus much of the postfire regeneration may have come from seeds from serotinous cones within the burn (Lotan 1976). With the exception of Engelmann spruce, the density vs. distance relationships were statistically significant at $P < 0.01$ or greater (Tomback and others 1990).

For the Saddle Mountain Burn, mean whitebark pine regeneration density was not significantly different than that for the Sleeping Child Burn, although somewhat lower (table 1). The density was actually comparable to that obtained for the ridgetop quadrats (west facing) in the Sleeping Child Burn. In contrast, the densities for subalpine fir and Engelmann spruce were much greater than those in the Sleeping Child Burn. Lodgepole pine was particularly abundant as well. Scatterplots of quadrat density vs. distance from the upper seed source were comparable to those from Sleeping Child (fig. 2).

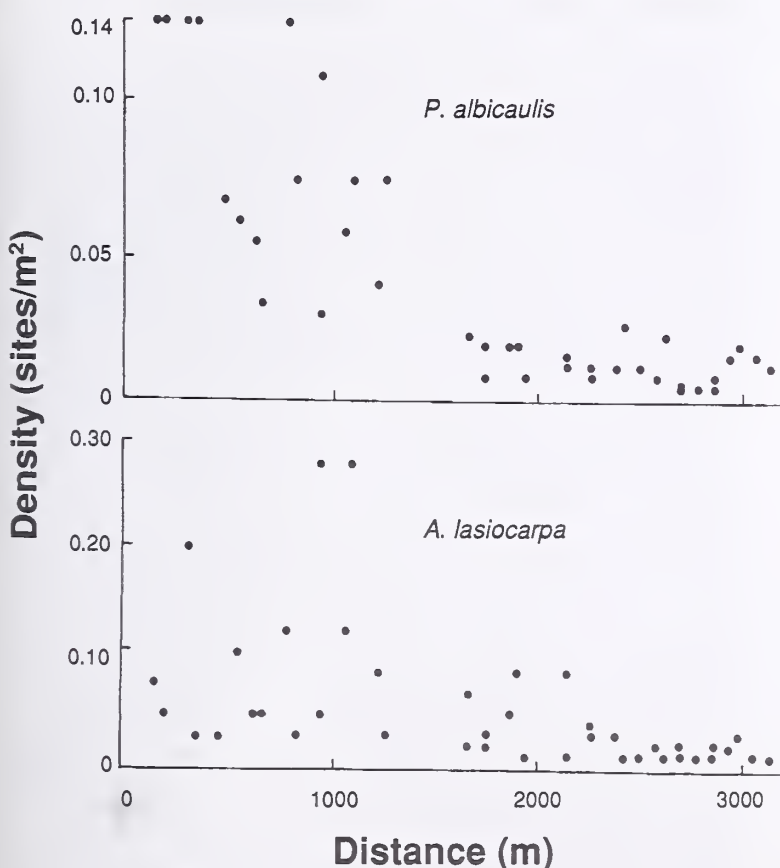


Figure 2—Scatterplots of regeneration density per quadrat versus distance from the whitebark pine seed source for whitebark pine (top) and subalpine fir (bottom) in the Saddle Mountain Burn. From Tomback and others (1990).

Table 2—Maximum age differences within clusters of whitebark pine seedlings. Cluster sample size for the Sleeping Child Burn = 87; for the Saddle Mountain Burn = 7. Based on table 4, Tomback and others (1993)

Maximum age differences	Sleeping Child		Saddle Mountain	
	Years	n	Percent	n
0		30	34.5	1
1		24	27.6	4
2		12	13.8	1
3		10	11.5	0
4		6	6.9	1
5		1	1.2	
6		1	1.2	
7		2	2.3	
8		1	1.2	

Whitebark pine regeneration showed a negative exponential distribution, and subalpine fir a similar but more linear negative relationship between quadrat density and distance from the upper, unburned forest (density vs. distance relationships significant at $P < 0.001$ for both). Similar to findings for the Sleeping Child Burn, the Engelmann spruce scatterplot was nearly flat. For both Douglas-fir and lodgepole pine, density increased with distance from the upper, unburned forest; major seed sources for both species were at the lower edges of the burn and, in the case of lodgepole pine, seeds from within the burn. However, the relationship between density and distance was not statistically significant for these latter three conifers.

The distinctive negative exponential shape of the whitebark pine regeneration curve probably results from two factors: (1) whitebark pine seeds are only available at the upper elevations of these burns, and (2) nutcrackers tend to bury higher densities of seeds near parent trees. Apparently, nutcrackers do cache seeds at long distances from parent whitebark pine trees, because we found low densities of regeneration up to 8 km from the whitebark pine seed source (Tomback and others 1990). It could be argued that the concomitant decrease in elevation in both study areas was a confounding variable in the whitebark pine density vs. distance relationship. However, recently, I tested this possibility by examining whitebark pine regeneration along a 3.4-km transect following an elevational isocline in the Sundance Burn of northern Idaho. Like the Sleeping Child and Saddle Mountain Burns, the whitebark pine seed source was restricted to one side of the burn, and the resulting regeneration curve followed a negative exponential distribution (Tomback 1992).

It appears that seed dispersal by nutcrackers has provided whitebark pine an advantage over its shade-tolerant competitor, subalpine fir, in the upper subalpine of the Sleeping Child Burn. Because wind-dispersed fir seeds from the upper seed source must travel against the prevailing winds and cover a long distance, the regeneration density of fir is lower than that for whitebark pine. In contrast, in the smaller Saddle Mountain Burn, whitebark pine and subalpine fir have comparable regeneration

densities. In this situation, dispersal of subalpine fir seeds (and Engelmann spruce seeds) is favored both by the prevailing winds from the west and the much smaller size of the burn. Thus, for restocking burns, seed dispersal by nutcrackers may provide whitebark pine an advantage over wind-dispersed conifers when (1) the size of the burn is large compared to distances traveled by wind-blown seeds, (2) the seed source is unfavorably positioned with respect to prevailing winds, and (3) the seed source is 1 km or more from the perimeter of the burn.

Another consequence of seed dispersal by nutcrackers is that seedling or sapling clusters occurred at more than 40 percent of the whitebark pine regeneration sites in both the Sleeping Child and Saddle Mountain Burns (Tomback and others 1990, 1993). Cluster sizes in the Sleeping Child Burn ranged from two to eight stems with an overall mean of 1.9 stems per regeneration site ($n = 455$ total sites). In the Saddle Mountain Burn, clusters ranged from two to 10 stems, with an overall mean of 2.0 stems per regeneration site ($n = 164$ sites). We aged two or more cluster members from a cluster subsample from each of the study areas (Tomback and others 1993). For the Sleeping Child Burn, there were no differences in age among seedlings within a cluster for 34 percent of the clusters, differences of 1 year for 28 percent of the clusters, and differences of 2 to 8 years within clusters for the rest of the subsample (total $n = 87$ clusters; all seedlings aged in 63 clusters) (table 2). Of the small number of clusters sampled in the Saddle Mountain Burn, five clusters (71 percent) had age differences of 0 to 1 year, and the remaining two clusters had seedlings differing by 2 and 4 years, respectively (table 2). These results strongly suggest that asynchronous germination of seeds may occur in some clusters. This could be explained by delayed maturation of some seeds or different sensitivities to environmental conditions. Laboratory (Leadem 1986; Pitel and Wang 1990) and experimental field studies (McCaughey 1993) indicate that embryo underdevelopment and delayed germination are typical in whitebark pine seeds. Delayed germination of seed caches would result in seedling establishment following little or no cone production and, thus, continuity of regeneration over time.

We compared age structure (year of tree establishment vs. time since fire) of regeneration for whitebark pine and subalpine fir in both the Sleeping Child and Saddle Mountain Burns to determine any important differences (Tomback and others 1993). Both species appeared to be similarly affected by environmental and ecological factors: a disproportionately high percentage of regeneration was established between 1977 and 1985, about 17 to 25 years after fire (see fig. 1 in Tomback and others 1993). Thus, major tree recruitment was episodic. A small increase in mean January through August precipitation between 1977 and 1985 possibly contributed to this trend. If we can generalize from these results, it appears that whitebark pine and subalpine fir become established synchronously after fire, albeit at different densities depending on relative seed dispersal abilities.

REGENERATION IN THE GREATER YELLOWSTONE AREA

Studies in the Greater Yellowstone Area following the major fires of 1988 have provided comparative information on patterns of seed dispersal, germination, and seedling mortality in seral whitebark pine communities (Tomback 1991, 1993). Unlike the large-scale, stand-replacing burns described earlier for western Montana, the Yellowstone fires created patches of burned areas of different severities, often surrounded by unburned forest.

In 1990, my research assistants and I established a total of 275 permanent plots, each 20 m², in two different study areas. In the Cooke City study area, Gallatin National Forest, we placed plots in four sample sites, representing the following treatments: dry, severely burned (50 plots); moist, severely burned (50 plots); dry, unburned (25 plots); moist, unburned (25 plots). Plot aspects in this area ranged from 80° to 180°, and elevations ranged from 2,680 to 2,745 m. On Mount Washburn, Yellowstone National Park, we selected three sample sites, representing the following treatments: dry, severely burned (50 plots); moist, severely burned (50 plots); moist, moderately burned (25). Aspects ranged from 250° to 360°, and elevations ranged from 2,560 to 2,745 m. All conifer regeneration was recorded for these plots in the summers of 1990, 1991, and 1992; whitebark pine regeneration was mapped for each plot. I briefly summarize the results here (Tomback 1991, 1993).

Whitebark Regeneration Trends

Despite an abundant whitebark pine cone crop in 1989, no whitebark pine regeneration occurred on any severely burned or moderately burned plots in 1990 in either study area (table 3). Only one plot in the moist, unburned treatment had one newly germinated seedling cluster. Although there was virtually no cone production in 1990, all severely burned and moderately burned treatments had some new whitebark pine regeneration in 1991, which was probably the result of delayed germination of seeds cached in 1989. Of the unburned treatments, again only the moist plots experienced any new regeneration (table 3).

In 1992 there was some new whitebark pine regeneration on the Cooke City moist, severely burned plots and on the Mount Washburn moist, moderately burned plots. By 1992, the latter sample site supported the highest density of whitebark pine regeneration of all sites (table 3). Seedling survivorship from 1991 to 1992 was fairly high. Those that survived to the summer of 1992 tended to be shaded by other plants or forest debris for at least part of the day. One cluster of seedlings that germinated in 1991 just outside a plot on the Mount Washburn moist, severely burned sample site contained two new germinants in 1992. This observation confirms the possibility that seeds within caches may germinate in different years, as illustrated by the ages of cluster members from western Montana.

Table 3—Whitebark pine regeneration densities for different plot treatments in the Cooke City and Mount Washburn study areas following the 1988 Yellowstone fires

Treatment	Mean density of regeneration sites ¹ per m ²		
	1990	1991	1992
Cooke City			
Dry, severely burned	0	0.012	0.015
Moist, severely burned	0	.014	.010
Dry, unburned	0	0	.002
Moist, unburned	0.002	.010	.008
Mount Washburn			
Dry, severely burned	0	.010	.011
Moist, severely burned	0	.021	.016
Moist, moderately burned	0	.030	.038

¹A single regeneration site may support either a single seedling or a cluster of seedlings arising from one seed cache.

Regeneration Trends of Other Conifers

Trends in the regeneration of other conifers differed between the Cooke City and Mount Washburn study areas, probably as a result of seed availability and seedbed conditions. For example, no conifer regeneration, old or new, occurred on the Cooke City dry, severely burned plots in 1990; small numbers of Engelmann spruce and subalpine fir occurred on these plots in subsequent years. On the moist, severely burned plots, new spruce germinants dominated in 1990 and both spruce and fir, new and old, in subsequent years. Primarily new fir regeneration occurred each year on the Cooke City dry, unburned plots, with few older firs surviving; and, mostly spruce occurred on the moist, unburned plots. Thus, spruce and fir regeneration predominated in the Cooke City area. Few lodgepole pine were apparent in the prefire forest or in the unburned forest around the treatment sites.

In the Mount Washburn study area, old and new lodgepole pine and new Engelmann spruce occurred in 1990 on the dry, severely burned plots. Older lodgepole pine and some new spruce occurred in subsequent years. On the moist, severely burned plots, new lodgepole pine and spruce regeneration predominated in 1990, and older lodgepole pine and spruce in 1991. In 1992 there were numerous new germinants of both species and some subalpine fir. High numbers of new spruce seedlings dominated the moist, moderately burned plots in 1990, and older and new spruce in subsequent years. Thus, lodgepole pine and spruce regeneration predominated in the burned area sampled on Mount Washburn. Lodgepole pine had been an important species in the prefire forest and was present, along with spruce, in unburned forest not far from the plot treatment sites. The high spruce regeneration density on the moderately burned plots may have been the consequence of a more favorable seedbed.

Although the numbers of whitebark pine germinants were lower in most cases than those of the other conifer species in both study areas, their survivorship from 1991

to 1992 was relatively high. The microsites selected for seed caching by nutcrackers and the hardiness of the whitebark pine seedlings may result in lower mortality compared to other conifers. We must follow the regeneration patterns of whitebark pine and its forest associates for several more years to test this idea.

CONCLUSIONS

The patterns of whitebark pine regeneration that we observe are the consequence of the seed-dispersal behaviors and site preferences of nutcrackers, as well as their tendency to bury multiseed caches. Nutcrackers bury seeds in burned terrain soon after fire (for example, see Tomback and Knowles 1989). Because whitebark pine seeds vary in maturation rate, nutcrackers cache both developed and underdeveloped seeds (Leadem 1986), resulting in germination over several different years from the same seed crop.

Early postfire regeneration of whitebark pine may be the consequence of rapid and widespread seed dispersal by nutcrackers, suitability of the cache sites selected by nutcrackers, and the hardiness of the seedlings themselves.

ACKNOWLEDGMENTS

The Intermountain Research Station, USDA Forest Service, Ogden, UT, has funded all whitebark pine postfire regeneration studies in western Montana, northern Idaho, and the Greater Yellowstone Area. I thank Stephen Arno, Jim Brown, and Bob Keane of the Intermountain Research Station Fire Sciences Laboratory, Missoula, MT, for logistic support and many helpful discussions concerning this research. Steve Arno and Bob Keane reviewed the draft manuscript. Lyn Hoffmann and Sharren Reuss (Sund) provided assistance during the western Montana studies, Kathy Carsey and Mary Powell worked with me during the three field seasons of the Yellowstone study, and Mary Powell, Jane Kees, and Mark Flower were field assistants for the Idaho work. Support for attending the SSPE Workshop was provided by the College of Liberal Arts and Sciences, University of Colorado at Denver.

REFERENCES

- Arno, S. F. 1980. Forest fire history in the northern Rockies. *Journal of Forestry*. 78(8): 460-465.
- Arno, S. F. 1986. Whitebark pine cone crops—a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-94.
- Arno, S. F.; Petersen, T. D. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. Res. Pap. INT-301. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 8 p.
- Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

- Finklin, A. I. 1983. Weather and climate of the Selway-Bitterroot Wilderness. Moscow, ID: University Press of Idaho. 144 p.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Leadem, C. L. 1986. Seed dormancy in three *Pinus* species of the Inland Mountain West. In: Shearer, R. C., comp. Proceedings—conifer tree seed in the Inland Mountain West symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 117-124.
- Lotan, J. E. 1976. Cone serotiny—fire relationships in lodgepole pine. In: Lyon, L. J., comp. Tall Timbers Fire Ecology Conference No. 14 and Intermountain Fire Research Council fire and land management symposium: proceedings; Missoula, MT: 267-278.
- McCaughey, W. W.; Schmidt, W. C.; Shearer, R. C. 1986. Seed dispersal characteristics of conifers in the Inland Mountain West. In: Shearer, R. C., comp. Proceedings—conifer tree seed in the Inland Mountain West symposium; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 50-62.
- McCaughey, W. W. 1993. Delayed germination and seedling emergence of *Pinus albicaulis* in a high elevation clearcut in Montana, USA. In: Edwards, D. G., comp. Seed dormancy and barriers to germination: proceedings IUFRO symposium; 1991 April 23-26; Victoria, BC. Victoria, BC: Forestry Canada. [In press].
- Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.
- Pitel, J. A.; Wang, B. S. P. 1990. Physical and chemical treatments to improve germination of whitebark pine seeds. In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 130-133.
- Romme, W. H. 1980. Fire frequency in subalpine forests of Yellowstone National Park. In: Fire history workshop: proceedings; 1984 October 20-24; Tucson, AZ. Gen. Tech. Rep. RM-81. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 27-30.
- Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. *The Living Bird*. 16: 123-161.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology*. 51: 451-467.
- Tomback, D. F. 1991. Progress report on 1991 fieldwork to U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT: patterns of postfire regeneration of whitebark pine in the Greater Yellowstone Area.
- Tomback, D. F. 1992. Patterns of postfire whitebark pine regeneration in the Sundance Burn of northern Idaho. Unpublished data on file at: Department of Biology, University of Colorado at Denver, Denver, CO.
- Tomback, D. F. 1993. Progress report on 1992 fieldwork to U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT: patterns of postfire regeneration of whitebark pine in the Greater Yellowstone Area.
- Tomback, D. F.; Knowles, J. W. 1989. Observations on nutcracker seed harvesting and caching on Mount Washburn following the 1988 Yellowstone fires. Unpublished data on file at: Department of Biology, University of Colorado at Denver, Denver, CO.
- Tomback, D. F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology*. 4: 185-219.
- Tomback, D. F.; Hoffmann, L. A.; Sund, S. K. 1990. Coevolution of nutcrackers and pines: implications for forest regeneration. In: Schmidt, W. C.; McDonald, K. J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-129.
- Tomback, D. F.; Sund, S. K.; Hoffmann, L. A. 1993. Post-fire regeneration of *Pinus albicaulis*: height-age relationships, age structure, and microsite characteristics. *Canadian Journal of Forest Research*. 23: 113-119.
- Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs*. 47: 89-111.

NEW TREND IN DENDROCHRONOLOGY: 1. THEORETICAL PRINCIPLES OF REPROCHRONOLOGY

Vladislav N. Vorobjev

Abstract—Reviews previous research pertinent to tree growth and cone-bearing relationships in Siberian stone pine (*Pinus sibirica*) and other species. The ultimate objective is to secure stable and moderately high cone production without significantly jeopardizing tree growth. To reach this objective the author points out potential avenues of research in tree growth dynamics and reproductive activities, utilizing procedures used in dendrochronology.

Dendrochronology was established as a science of the growth dynamics of trees, the structure of the annual ring, and the effect of internal and, especially, external factors. The latter determined the development of dendrochronology and a number of other special scientific areas.

Generative processes have been studied separately and dealt with by the corresponding branch of seed farming in terms of the concept of the crop dynamics or crop cyclicity. In doing so, novel independent results have been obtained and, more important, premises have been created for combining these findings with dendrochronology.

The correlation between the growth and generative development of higher plants comprises a number of aspects and has been studied for a long time. The study of herbaceous plants has lagged behind that of tree investigations. Suffice it to say that not only have monographs on this subject been lacking, but original publications contributing to this field have also been scarce. The only exception, to the best of our knowledge, has been the work done in Tomsk by the laboratory of cone-bearing trees (Goroshkevich 1989; Nekrasova 1974; Vorobjev 1983; Vorobjev and Vorobjeva 1982; Vorobjev and others 1989). However, the problem of the relation between growth and cone bearing (in coniferous trees, in particular) is of great importance in view of the necessity to increase cone crops. While this problem is being solved in herbaceous plants and fruit-bearing trees by an intense short-term shift of metabolism toward activation of the generative processes, this technique fails in coniferous trees because of the long growth period inherent in them.

It is assumed on the basis of the foregoing considerations that control of the sexual reproduction of trees

must be related to the determination of optimal correlations between the generative and growth processes through the long-term activation of the vital activity of plants.

PREVIOUS RESULTS

The expedience of this approach was also confirmed by the results of our previous investigations. The experiments on the resin tapping of the Siberian cedar pine, sometimes called Siberian stone pine (*Pinus sibirica*), showed that the increase of cone crops by creating favorable conditions for cone bearing alone had no future because it would eventually result in the weakening of the growth processes and then of the generative ones (Vorobjev 1974). Therefore, it appears necessary to look for certain correlations between growth and cone bearing that would make it possible to secure moderately high cone crops on a long-term stable basis. It is this problem that seems to be of great theoretical and practical interest (Vorobjev and Vorobjeva 1980).

The study of the effect of the reproductive activity on shoot growth and the shoot condition on subsequent cone bearing provides insight into the relation between tree growth and cone bearing. Observations have shown that cone bearing depends on the previous shoot growth in Scotch pine (*Pinus sylvestris*), English oak (*Quercus* sp.), and apple (*Malus* sp.) trees (Minina 1954; Polozova 1957; Pravdin 1950; Tsel'niker and Semikhatova 1957). It has been pointed out that optimal shoot growth is required to induce cone bearing. Of no less importance is the time it takes to achieve growth, since the flower germs are initiated when apical growth gets weaker or terminates. The surface area of leaves also plays a significant role.

The effect of cone bearing on the current increment has been the subject of a number of papers. In particular, the diameter increment in coniferous trees was shown to decrease in the cone-maturing year (Chalupka and others 1975, 1976, 1977; Danilov 1953). However, the effect of the decreased diameter increment on further seminference of trees and metamere growth has not been examined yet.

The change in shoot growth due to cone bearing is the net effect of sexualization and subsequent development of generative organs at different stages of their maturity. The dependence of the cambial growth of the shoot on its sex has been described in literature (Nekrasova 1972; Varnell 1976). However, no experimental evidence of the role of sexualization and nutrition of the generative organs, and of the effect of the nutrition of the 1- or 2-year cones on the annual ring and its internal structure in the growing shoot has been available (Vorobjev and Vorobjeva 1982).

Poster presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Vladislav N. Vorobjev is Head of the Academy of Sciences, Siberian Branch, Institute for Ecology of Natural Complexes, Akademicheskyy pr. 2, Akademgorodok, Tomsk, 634055, Russia.

RETROSPECTIVE METHOD

Good possibilities for the study of the effect of cone crops on tree increment (both linear and cambial) have opened up due to recent development of the method of retrospective account of the reproductive activity of trees during their lifetime (see Vorobjev and others, these proceedings). Significantly, this procedure can also be used to reproduce male "flowering" and the formation of a number of vegetative metameres, though for a shorter period of time. In this case, shoots, branches, and crown become major objects of inquiry in the investigation of the relation between the growth and generative development of trees.

The research done into the growth-cone-bearing relationship in Siberian cedar pine in West Siberia and Gorny Altai for the last 100 years or more (Vorobjev 1983) suggests a new trend in the investigations made at the crossroads of the two sciences, biology of reproductive development and dendrochronology.

This trend can be referred to as reprochronology, comprising both the cyclic fluctuations of the reproductive activity and its relation to the cambial growth. Perhaps, the word is not a happy choice from the terminology point of view, but it generally implies sexual reproduction.

The time series of reproductive activity studied show cycles of variable duration ranging from 3 to 28 years or more. A 10- to 11-year reproductive cycle is less pronounced than the growth cycle. The relation between the crop dynamics and solar activity is feebly marked, and seed cycles fall both at the peak and decay of the solar activity. The reproductive activity is indirectly related to the cambial growth and is delayed with respect to the latter by the time interval determined by the life cycle of one generation and the growth aftereffect. The peak of the seminiference activity generally falls at the descending branch of the solar cycle and the period of the retarded shoot growth. An increase in cone crops is related to the previous solar activity and vigorous growth.

Thus it appears worthwhile to study further the structure of the time series of the reproductive activity and their relation to the dynamics of growth of shoots, branches, and trees, to evaluate the effect of the external factors using new methods, and to develop prediction models. Also of scientific importance are individual, interpopulational, geographical, ecological, and other aspects of the relation between the growth and the generative development of trees as well as between the seminiference and the annual ring of the shoot and tree. It should be noted that the foregoing potential research areas suggest the use of the techniques and procedures adopted in dendrochronology.

REFERENCES

- Chalupka, W.; Giertych, M.; Krolikowski, Z. 1975. The effect of cone crops on growth in Norway spruce (*Picea abies* (L.) Karst.). *Arbor. Kor.* 20: 201-212.
- Chalupka, W.; Giertych, M.; Krolikowski, Z. 1976. The effect of cone crops in Scotch pine on tree diameter increment. *Arbor. Kor.* 21: 361-366.
- Chalupka, W.; Giertych, M.; Krolikowski, Z. 1977. Relation between specific gravity of wood in Norway spruce (*Picea abies* (L.) Karst.): some growth parameters and cone yield. *Arbor. Kor.* 22: 205-212.
- Danilov, D. N. 1953. Effect of cone-bearing on tree-ring structure in common spruce (*Picea excelsa*). *Bot. J.* 38(3): 367-377. [In Russian].
- Goroshkevich, S. N. 1989. The dynamics of the microstrobile initiation in the male shoots of the Siberian cedar pine as related to weather conditions. *Ecol.* 6: 33-39. [In Russian].
- Minina, E. G. 1954. Biological principles of flowering and fruiting oak. *Transactions of Inst. of Forest of USSR Acad. of Sci.* 17: 5-97. [In Russian].
- Nekrasova, T. P. 1972. Biological principles of seminiference of Siberian cedar pine. *Novosibirsk: Nauka.* 272 p. [In Russian].
- Nekrasova, T. P. 1974. The cyclicity of the cone-bearing of Siberian cedar pine. In: *Biology of seed reproduction of coniferous trees of West Siberia.* Novosibirsk: Nauka: 70-75. [In Russian].
- Polozova, (L.) Y. 1957. Growth of oak shoots as related to fruiting processes. *Letters of Inst. of Forest of USSR Acad. of Sci.* 9: 9-17. [In Russian].
- Pravdin, (L.) F. 1950. Sexual dimorphism in Scotch pine (*Pinus sylvestris* L.). *Transactions of Inst. of Forest of USSR Acad. of Sci.* 3: 190-201. [In Russian].
- Tsel'niker, Y. L.; Semikhatova, O. A. 1957. On the relation between vegetative and generative stages of shoot development in certain trees. *Bot. J.* 42(7): 1044-1054. [In Russian].
- Varnell, R. J. 1976. Correlation between branch characteristics and production of female strobile in longleaf pine. *Forest Science.* 22(2): 159-161.
- Vorobjev, V. N. 1974. Growth and generative processes in Siberian cedar pine under metabolic disturbance. In: *Biology of seed reproduction of coniferous trees of West Siberia.* Novosibirsk: Nauka: 140-170. [In Russian].
- Vorobjev, V. N. 1983. Biological principles of comprehensive utilization of Siberian cedar pine forests. *Novosibirsk: Nauka.* 254 p. [In Russian].
- Vorobjev, V. N.; Vorobjeva, N. A. 1980. On the problem of regulation of seed crops of coniferous trees. In: *Selection, genetics and seed farming of trees as the basis for forming of highly productive forests.* Moscow: 391-395. [In Russian].
- Vorobjev, V. N.; Vorobjeva, N. A.; Goroshkevich, S. N. 1989. Growth and sex of Siberian cedar pine. *Novosibirsk: Nauka.* 167 p. [In Russian].
- Vorobjeva, N. A.; Vorobjev, V. N. 1982. The effect of female generative organs on the shoot growth in the Siberian cedar pine. *Lesovedeneye (For. Sci.)* 1: 51-57. [In Russian].

NEW TREND IN DENDROCHRONOLOGY: 2. METHOD OF RETROSPECTIVE STUDY OF SEMINIFERENCE DYNAMICS IN PINACEAE

V. N. Vorobjev
S. N. Goroshkevich
D. A. Savchuk

Abstract—Introduces a new method of retrospective analysis of cone crop dynamics of Siberian stone pine (*Pinus sibirica*) for up to 100 years before the present. For about the first 20 years, cone abscissions are discernible on the exterior of the shoots and can be used to reconstruct cone crop production, but after this they are not identifiable. A method was developed utilizing cross-sectional saw cuts to examine the interior of the branch shoots. Traces of the abscissions of cones remain in the shoots and, consequently, cone crops can be reconstructed for virtually the entire life of the tree with the procedures described in this paper. This method may also be useful for other conifers.

A retrospective study of the life activity of trees has always been of great interest to scientists. Retrospective analysis has been widely practiced in dendrochronologic and dendroclimatic studies focusing on the investigation of tree rings whose structure and dimensions are important indicators of the life activity of the tree organism. The variations of tree increment observed are basically related to the effect of exogenic factors, and climatic conditions in particular. As to the endogenic factors and, primarily, the reproductive activity, their contribution is recognized but not accounted for because of the difficulty of estimating cone crops for long periods of time. In fact, this aspect of activity of the tree organism is regarded as the so-called "white noise" in a multifactor dendrochronological analysis of the effect of different conditions.

The early information on the annual dynamics of cone crops has been obtained from direct counts of the number of generative organs for several years. This technique is fairly widely used even today. However, applications of this technique are limited due to the necessity of long-term observations. Naturally, scientists sought to develop a method of retrospective study of the cone crop dynamics. This method is based on the fact that the cones and fruits either remain on the branches after the seed abscission or fall out, leaving traces on the shoot bark. The seasonal

character of the shoot growth in trees in the temperate zone makes it possible to age each shoot and, consequently, its generative organs.

The first information we are aware of on the use of the retrospective method of studying the crop dynamics can be found in the work of A. Renvall (1912) for the Scotch pine and N. Nesterov (1914) for some leaf-bearing trees (oak, maple, hawthorn). The method was further developed and elaborated in great detail by Z. Trofimova (1953), T. Nekrasova (1957), and P. Gorchakovskiy (1958) for different coniferous trees. A most comprehensive description of this method was given by A. Korchagin (1960).

The advent of the retrospective method has facilitated significant progress in the investigation of crop dynamics. The latter can be reproduced for the past 10-15 years on the basis of the cone traces on the shoot bark. Special emphasis has been placed on Siberian cedar pine (sometimes called Siberian stone pine) because of the great natural and economic importance of its seed crops (Iroshnikov 1963; Vorobjev 1964, 1974). As a result, a cyclic character of the fluctuations in the crops for different years was revealed and the relations between the seminiference, weather conditions, and tree growth were examined. However, further advance of the investigations required that the methodology be improved.

In our opinion, there are two very essential ways of improving the method. First, work out a special technique for reconstructing the stages of the development of each generation from the initiation to the complete maturation of cones and to determine the number of cones that prematurely abscissed in different stages of their development. These data will make it possible to study the crop dynamics and, in particular, its effect on the tree and shoot growth and the annual ring structure. Second, extend the period of the retrospective account of crops from 10-15 years to 100 years or more.

The object of the present paper is to introduce a new method of retrospective analysis of the seminiference dynamics of Siberian cedar pine, making use of the foregoing information.

CONE DEVELOPMENT

Cones in the Siberian cedar pine are initiated in late July or early August (Nekrasova 1972). The germs of the female cones hibernate in the form of undifferentiated

Poster presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

V. N. Vorobjev is Head of and S. N. Goroshkevich and D. A. Savchuk are Members of the Academy of Sciences, Siberian Branch, Institute for Ecology of Natural Complexes, 2, Academicchesky pr., Akademgorodok, Tomsk, 634055, Russia.

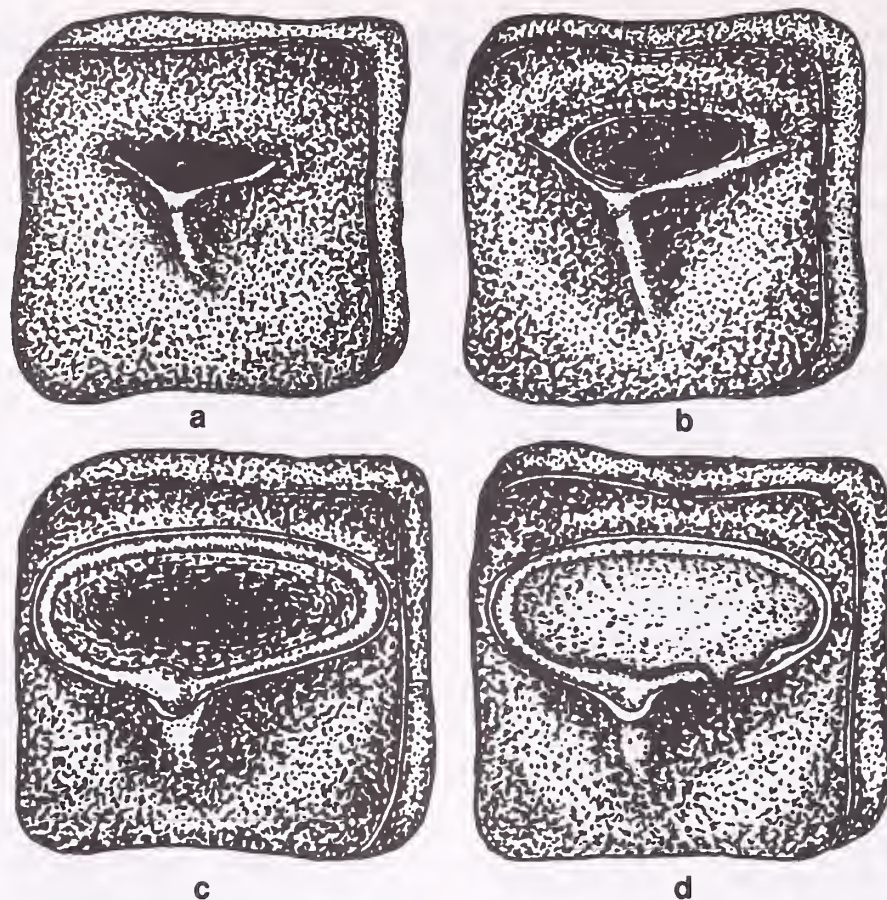


Figure 1—Female cone traces on the shoot bark. x 6:
(a) cone that abscised before pollination, (b) cone that abscised after pollination, (c) cone that abscised during maturation, (d) mature cone.

primordia surrounded by bud scales. The primordia are located in the distal part of the winter terminal bud. The development of the female cones begins in May. An active linear growth of shoots occurs in the first half of June, and the cones resemble large lateral buds in the distal part of the growing shoot. Special observations show that the development of some of the female cones ceases at this period of time and they abort. For example, normally developing cones were bright green and 10-15 mm long in a Siberian cedar pine forest near a settlement in the south of the Tomsk region on June 6, 1990. Some of the female buds began to burst, while others were of much smaller size. In the latter case, a longitudinal section of a germ showed that it had died in the differentiation phase. It looked like a small (1.5-2.0 mm) brown protuberance. After the degeneration of the germinal cone the bud dries up and abscises. Abortive female buds leave small (2.5-3.0 mm) dark triangular traces (fig. 1a).

Pollination in Siberian cedar pine generally occurs in the second half of July (Nekrasova 1972). After pollination the cones grow for some time until they are 2 mm long. During this period (June-July) the cones may also cease their development and abort. Traces of cones that abscised shortly after the pollination are larger (4-5 mm), and more roundish than those of the abortive female buds and are relatively smooth surfaced (fig. 1b).

In the year of maturation both the cones and shoots grow larger. The cones reach their ultimate dimensions by the time of fertilization (June 15-20) (Nekrasova 1972). Therefore, the cones that abscise in the process of maturation (June-August) leave the traces of the same shape and size as normal mature cones do. The traces are large (up to 7-8 mm) and oval with a funnel-shaped inner surface (fig. 1c, d). Mature cones abscise in late August or early September. The inner surface of their traces on the shoot bark is covered with resin (fig. 1d).

TRACE IDENTIFICATION

The identification of cone traces would require knowledge of the morphostructure of the mature shoot and the origin of its different parts. The annual shoot in large cone-bearing branches in Siberian cedar pine consists of two elementary shoots (Vorobjev and others 1989). The first (spring) shoot develops from the winter bud in June. The second (summer) shoot is initiated in June and is found to enlarge at the beginning of July. Each elementary shoot has short shoots (brachyblasts) and lateral extending shoots. The length of the axis and the number of its metameres in the spring shoot are approximately ten times as large as in the summer shoot. The female cones are located in the distal part of the spring shoot. Small lateral vegetative shoots usually grow at the same level

as the female cones. However, there may be no lateral shoots. The main whorl of large lateral shoots is located on the summer shoot. It should be noted that summer shoots in mature trees are formed when the spring shoot bears cones. Therefore, the summer shoot can be regarded as an indirect evidence of the presence of cones in the spring shoot. The traces of mature cones on mature need-less shoots will occur in the distal part of each annual shoot under the main whorl of the lateral shoot.

The traces should be counted from the top of the branch to yield the number of different types of traces on each annual shoot. This procedure makes it possible to reconstruct the entire dynamic cycle of the initiation, development, and maturation of cones (over 10 to 12 years). The traces of abortive female buds on older shoots are destroyed because of the secondary bulge of the shoot axis and core cracking, which precludes their identification and count. Large traces of mature cones persist for a longer period of time, and they can be used for the reconstruction of crop dynamics over approximately 20 years.

SAMPLING

Our experience shows that it is necessary to sample 10 branches from one tree. The branches selected must be from different parts of the crown (top, middle, lower). Each branch must be no less than 20 years old. To reconstruct the dynamics of the initiation and development of cones on individual branches, one has to use branches of medium size and ignore the traces of cones on the lateral shoots. On the other hand, the seminference dynamics for the tree or stand as a whole can be followed by using cone-bearing branches of different size and, most important, by taking into account the traces on small lateral branches.

As the number of annual rings increases, the traces of cones on the bark in the cone-bearing branches of trees become indiscernible. Therefore, a procedure was developed for the identification of such traces on the cross-sectional saw cuts of branches (Vorobjev 1979). The saw cuts of the bases of whorls show that the traces of cones remain within shoots and are quite discernible, which makes it possible to reconstruct the crop dynamics virtually for the entire life of the tree. Thus, the time scale of the proposed procedure can be extended.

The saw cuts must be made 1 cm beneath the point where the longitudinal axis of the branch intersects the axes of the lateral shoots. Then they are paper-sanded and examined with a stereomicroscope $\times 16$. The saw cuts must begin with the whorls where the external traces on the bark are fairly visible. The identification of the inner traces should also begin with those whorls. This is especially important for the differentiation of different periods of cone development.

TRACE CHARACTERISTICS

The cone traces on the saw cuts of branches can be described as follows: The trace of the cone that abscised before pollination (the trace of the abortive female bud) has the form of a brown ray with a uniform width of

0.3 ± 0.03 mm and a length of 1.6 ± 0.2 mm. It runs from the pith of the shoot to its bark at the background of a yellow saw cut wood (fig. 2a). The trace of the cone that abscised after pollination and that of the immature cone are half as large edgewise as the trace of the cone that abscised before pollination. The latter trace (fig. 2b) in contrast to the former (fig. 2c) has a bulge at the end (1.7 times as large as the ray width) or is slightly forked. The trace of the mature cone (fig. 2d) is twice as large as that of the immature cone. Note that there may be no ray. The trace of the mature cone differs greatly from all the other traces (see fig. 2d and figs. 2a, b, c) by an oval or triangular bulge (2.4 ± 0.3 mm wide) at the ray end. Such traces are often accompanied by a specific deformation of the tree rings as a result of rupture of phloem and xylem tissues of the shoot by a great number of cones. Thus the more mature the cone the brighter and longer is its trace on the saw cut. The bulge is also larger.

The traces of cones differ from the traces of the lateral shoots and brachyblasts on the cross-sectional saw cuts. The trace of the lateral shoot (fig. 2e) is wide and generally runs toward the bark to join the shoot axis. The trace of the cone does not reach the bark. The trace of brachyblast (fig. 2f) is very similar to the trace of the cone that abscised before pollination (the abortive female bud), but the former trace is much longer (2.5 ± 0.2 mm) and its end grows narrower. The main thing is that the trace of brachyblast is surrounded by a brighter layer of wood ($3.8 \pm 0.3 \times 0.7 \pm 0.1$ mm), which is visible to a naked eye.

USE OF METHODS

We feel that use can be made of methods based on the difference in the density of the cone traces and that of the surrounding wood (roentgenography, densitography, laser techniques, etc.) in the cases where the traces on the saw cuts are dim (especially the traces of the prematurely abscised cones), or else, if the saw cut has been made in a wrong way. In particular, soft x-ray roentgenography of a 5- to 7-mm-thick saw cut of a branch (the time of exposure was 6 minutes) made it possible to determine unambiguously the structure of tree rings, cone traces, and those of other metameres (Vorobjev 1979). The above techniques provide documentary evidence for subsequent analysis.

This ability to distinguish the internal traces must be practiced using the branches with fairly visible external cone traces on the bark. The selection of the branches for the analysis must be made in the female zone of the crown. The branches with one top are most suitable for examining the relationship between the seminference and the shoot growth. For the study of crop dynamics, on the other hand, the branches with a few tops must be used. These branches often occur in the lower part of the female zone.

Sample branches of the tree must be taken from three age groups (30, 60, and 100 years old). The extreme values of the crop capacity (the number of cones on one shoot) are omitted in the case of young branches for the first few years before cone bearing and in the case of old branches for the last tens of years after cone bearing. The extremes are ignored because of the absence of cone

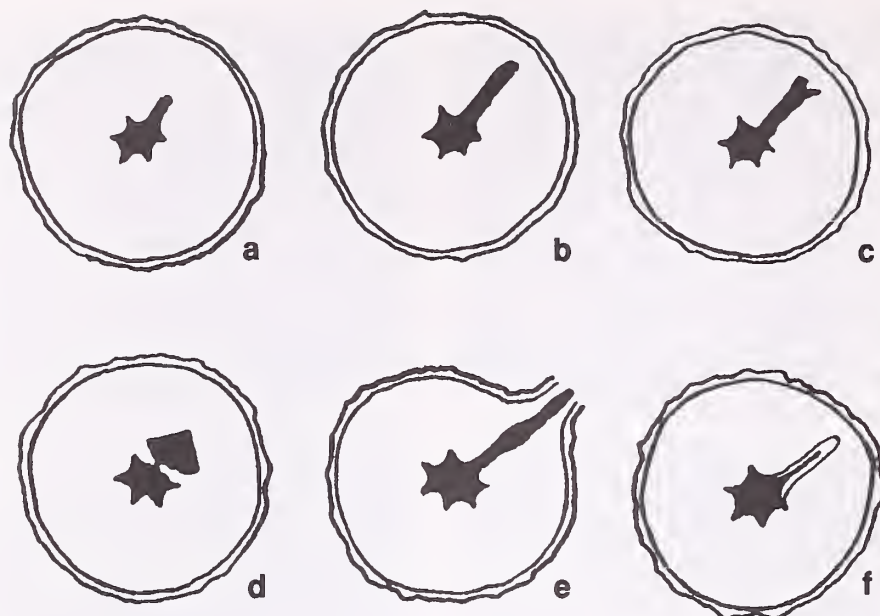


Figure 2—Traces of generative and vegetative organs on cross-sectional saw cuts of branches. x 3: (a) cone that abscised before pollination, (b) cone that abscised after pollination, (c) cone that abscised during maturation, (d) mature cone, (e) lateral shoot, (f) brachyblast.

traces. The information is taken into account within the number series, for it reflects nonseed years. The traces are hardly visible at this time because of the predominant abscission of 1-year-old conelets caused by early frosts or the lack of pollination.

No less than three to five 200- to 250-year-old trees of the first or second Kraft's class are to be selected from one sample area for the study of sample branches.

A retrospective study of the seminiference of Siberian cedar pine on the basis of the proposed method makes it possible to assess the effect of the reproductive activity of trees on the annual ring structure and size, to follow the crop cyclicity, to elaborate the ways of the long-term and super-long-term forecasting of crops, and to construct an ontogenetic model of the relationship between the growth and seminiference of shoots. This method appears applicable to other coniferous plants and, first and foremost, to Pinaceae.

REFERENCES

- Gorchakovsky, P. L. 1958. New issues in the method of investigation of the seminiference dynamics of coniferous trees. *Bot. Zhourn.* 43(10): 1445-1459. [In Russian].
- Iroshnikov, A. I. 1963. The cone-bearing of Siberian cedar pine in western Sayani. In: *Cone-bearing of Siberian cedar pine in eastern Siberia*; Moscow: Publ. of USSR Academy of Science: 104-119. [In Russian].
- Korchagin, A. A. 1960. Methods of account of seminiference of trees and forest communities. In: *Field Geobotany*; Moscow-Leningrad: Publication of USSR Academy of Science: Vol. 2: 41-133. [In Russian].
- Nekrasova, T. P. 1957. On the methods of investigation of cone-bearing dynamics in coniferous trees. *Izv. Vost. Fil. Akad. Nauk SSSR.* 6: 138-145. [In Russian].
- Nekrasova, T. P. 1972. *Biological principles of seminiference of Siberian cedar pine*. Novosibirsk, Nauka: 272 p. [In Russian].
- Nesterov, N. S. 1914. On the problem of the methods of investigation of cone-bearing of trees. *Forest-Industrial Vestnik.* Vol. 26. [In Russian].
- Renvall, A. 1912. *Die periodischen Erscheinungen der Reproduktion der Kiefer an der polaren Waldgrenze*. *Acta Forest Fenn.* 22(3): 130 p.
- Trofimova, Z. I. 1953. Determination of pine crops by biological method. *For. Econ.* 1: 67-69. [In Russian].
- Vorobjev, V. N. 1964. The cone-bearing of Siberian cedar pine in altitude subzones of north-eastern Altai. *Izv. Sib. Otd. Akad. Nauk SSSR, Ser. Biol.-Med. Nauk.* 12(3): 86-90. [In Russian].
- Vorobjev, V. N. 1974. Peculiarities of cone-bearing of siberian cedar pine in mountain conditions. In: *Biology of seed reproduction of coniferous trees of western Siberia*. Novosibirsk, Nauka: 15-70. [In Russian].
- Vorobjev, V. N. 1979. A method of retrospective study of seminiference dynamics in *Pinus sibirica* Du Tour (Pinaceae). *Bot. Zhourn.* 64(7): 971-974. [In Russian].
- Vorobjev, V. N.; Vorobjeva, N. A.; Goroshkevich, S. N. 1989. *Growth and sex of siberian cedar pine*. Novosibirsk, Nauka. 167 p. [In Russian].

Importance to Wildlife



International Workshop
St. Moritz 1992

NUTRITIVE VALUE OF WHITEBARK PINE SEEDS, AND THE QUESTION OF THEIR VARIABLE DORMANCY

Ronald M. Lanner
Barrie K. Gilbert

Abstract—Seeds of whitebark pine (*Pinus albicaulis*) are eaten year-round by their disperser, Clark's nutcracker (*Nucifraga columbiana*), and may be the only food that is fed to their young. They are also preferentially larder-hoarded by the red squirrel (*Tamiasciurus hudsonicus*); and are eaten in large quantities by black bears (*Ursus americanus*) and grizzly bears (*U. arctos*), especially prior to hibernation.

Analyses show whitebark pine seeds have a mean seed weight of 119 mg, of which kernels comprise 52.5 percent. Kernel content was approximately 21 percent carbohydrate, 21 percent protein, 52 percent fat, 3 percent ash, and 3 percent water. Major mineral nutrients present were Cu, Zn, Fe, Mn, Mg, and Ca. Sixteen amino acids were present, with glutamic acid, lysine, and arginine especially abundant. Major fatty acids were linoleic, oleic, and γ -linolenic, with lesser amounts of 11 others. The unsaturated fraction was 92 percent.

The variable period of dormancy is analyzed in terms of its contribution to fitness in a variable environment, its phylogenetic distribution within *Pinus* subg. *Strobus* and subsect. *Cembrae*, and its effect in retaining nutcracker populations by broadening the food base. The food base is broadened by the interaction of memory duration, seed crop frequency, and foraging on buried dormant seeds whose location is betrayed by presence of germinants. This may explain the excessive caching behavior of nutcrackers and may reduce the frequency of irruptions during times of food shortage. Even when seed crops are sporadic, variable dormancy can make seeds available to nutcrackers in most years, and as early as the first year after dispersal birds can forage on seeds cached by other birds.

Whitebark pine (*Pinus albicaulis* Engelm.) is the only North American member of *Pinus* subsect. *Cembrae*, the stone pines. The species is found in subalpine habitats in the Northern Rocky Mountains of Canada and the United States, and in the Cascade Mountains-Sierra Nevada system (Critchfield and Little 1966). Because whitebark pine usually grows in inaccessible areas and has relatively low commercial value, it was long neglected by researchers. But in recent years, due largely to interest in corvid-pine mutualisms stimulated by a seminal review (Turcek and

Kelso 1968), it has received greatly increased attention. Much of this attention has focused on the important role of whitebark pine seed in the biology of animals that inhabit the whitebark pine forest.

It is the large lipid-rich "nut" of this pine that attracts its seed disperser, Clark's nutcracker (*Nucifraga columbiana*) (Tomback 1978). Evidence indicates that the pine can reliably regenerate only from seeds cached in the soil by its nutcracker mutualist (Hutchins and Lanner 1982), and that these seeds are the sole nutritional resource for nutcrackers throughout their juvenile stage (Vander Wall and Hutchins 1983). Further, it has been shown that whitebark pine seeds are a preferred food of the red squirrel (*Tamiasciurus hudsonicus*), which larder-hoards great quantities of cones on and below the ground (Hutchins and Lanner 1982). Both black bears (*Ursus americanus*) and grizzly bears (*U. arctos*) raid the squirrel middens in order to gorge themselves with pine nuts both before and after hibernation (Kendall 1983; Mattson and Jonkel 1990). Thus the whitebark pine seed is of obviously great nutritional importance to at least five organisms of its ecosystem: Clark's nutcracker, the red squirrel, black and grizzly bears, and whitebark pine itself, for whose benefit the seed originally evolved. It is therefore of more than passing interest to know the nutrient content of this valued seed.

Published analyses of whitebark pine nuts have stressed their high caloric value, which is mainly a function of high lipid content. Emphasis on caloric content appears to be a response to the current ecological fixation on energetics of food resources, almost to the exclusion of other food characteristics. Thus Lanner (1982) has documented the partitioning of energy in nuts and other cone components, and Hutchins and Lanner (1982) have reported changes in the caloric value of whitebark pine seeds as the seeds mature, but other aspects of the nutritional qualities of these seeds have been neglected.

Another characteristic of the whitebark pine seed that requires attention is its variable dormancy. Seeds of several *Cembrae* species have been reported to delay germination until the second or third year following dispersal (USDA FS 1974). This has been attributed to the immaturity of embryos at the normal germination date, and has been blamed for low germination rates of whitebark pine seeds in laboratory tests (Pitel and Wang 1990). Kozlowski and Gunn (1972) have suggested that germination delays ensure establishment "even though the early germinants failed to survive severe environmental stresses such as droughts or severe frosts," but they offer no data to support this intuitively attractive idea. According to McCaughey (1992), whitebark pine seeds of a cohort displayed germination

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Ronald M. Lanner is Professor, Department of Forest Resources, and Barrie K. Gilbert is Senior Scientist, Department of Fisheries and Wildlife, both at Utah State University, Logan, UT.

during the first (11 percent), second (45 percent), third (11 percent), and fourth (percent not specified) postdispersal years.

The objectives of this paper are to document the nutritional characteristics of whitebark pine seeds, and to suggest some possible ramifications of the variable dormancy habit.

SEED COMPOSITION ANALYSES

Analyses were made of whitebark pine seeds of the 1989 crop from around Gardiner, MT (2,635 m elevation), provided by Dr. Ward McCaughey of the Intermountain Research Station (USDA Forest Service), Bozeman, MT.

Protein determination was made by the Kjeldahl method, fat determination by the chloroform methanol method of Hubbard (1977), and mineral assays by atomic absorption by Drs. Arthur Mahoney and Dejie Zhang, Department of Nutrition and Food Sciences, Utah State University. Five samples were used for these determinations. Amino acid analyses of nut protein were made by Dr. Rod Brown, Department of Nutrition and Food Sciences, Utah State University, using a Beckmann 6300 amino acid analyzer. Four runs were made: data presented here are the means of those runs. Fatty acid composition of kernel fats was provided by Laurence G. Cool of Dr. E. Zavarin's laboratory at the Forest Products Laboratory, University of California, Richmond, CA, and was determined by gas chromatography.

Results

Kernel Composition—Mean values of 20-seed samples yielded the following seed coat versus kernel (female gametophyte plus embryo) breakdown: seed coat, 47.5 percent, 0.0568 g; kernel, 52.5 percent, 0.0626 g. Kernels consisted of water (3.5 percent), ash (2.8 percent), carbohydrates (21 percent) [calculated value], protein (21 percent), and

Table 2—Comparative abundance of amino acids identified in kernel protein of three pine species¹

Amino acid ²	<i>P. albicaulis</i>	<i>P. edulis</i>	<i>P. pinea</i>
GLU	100	87	87
LYS	91	19	19
ARG	76	100	100
ASP	58	47	47
GLY	53	26	26
VAL	52	27	26
ALA	51	27	27
LEU	51	37	37
SER	50	22	22
PRO	48	28	28
ISO	34	20	20
PHE	26	20	20
TYR	23	19	19
THR	20	16	16
HIS	17	12	12
MET	5	9	9
CYS	—	9	9
TRY	—	6	1

¹Species and references: *P. albicaulis* (this paper), *P. edulis* (McCarthy and Matthews 1984), *P. pinea* (McCarthy and Matthews 1984).

²Amino acids not previously mentioned: CYS = cystine, TRY = tryptophan.

fat (52 percent). Atomic absorption analysis disclosed the following mineral composition, in micrograms per gram of ash: Cu, 17.5; Zn, 66.9; Fe, 35.7; Mn, 132; Mg, 17.5; Ca, 51.9.

Amino Acids—Sixteen amino acids were identified in the whitebark pine kernel samples. The most abundant were glutamic acid, lysine, arginine, and aspartic acid (table 1). These ranged from 0.42 to 0.73 nmol/mg. Also abundant, ranging from 0.35 to 0.39 nmol/mg were glycine, valine, alanine, leucine, serine, and proline. Lesser quantities were found of isoleucine, phenylalanine, tyrosine, threonine, and histidine; and least of methionine (table 1).

Amino acid quantities have been expressed in the literature in various ways. Therefore, to compare the amino acids of whitebark pine with those of other species, we have given the most abundant amino acid of each species the index value of 100, and all others are scaled appropriately within each species. Thus, while the most abundant amino acid (100) of whitebark pine is glutamic acid, that of *Pinus edulis* and *P. pinea* is arginine (table 2).

Fatty Acids—Fifteen fatty acids were identified on the chromatograph. The most abundant of these were the polyunsaturated linoleic acid and monounsaturated oleic acid, which comprised 46.9 percent and 30.6 percent of the total fatty acid methyl esters, respectively. The other components are present in much smaller proportions (table 3). The total fraction of unsaturated fatty acids was 92.0 percent, 32.1 percent monounsaturated, and 59.9 percent polyunsaturated.

Discussion

Due to differences in analytical techniques, and variation in the multiplier used in determining protein content, the published fractions of fats, proteins, carbohydrates, and ash in nut kernels are quite variable.

Table 1—Amino acids identified in kernel protein of whitebark pine in order of abundance (mean of four runs)

Amino acid	Nanomoles per mg
Glutamic acid	0.729
Lysine	.666
Arginine	.554
Aspartic acid	.422
Glycine	.386
Valine	.380
Alanine	.373
Leucine	.369
Serine	.363
Proline	.352
Isoleucine	.245
Phenylalanine	.192
Tyrosine	.168
Threonine	.147
Histidine	.126
Methionine	.038

Table 3—Fatty acids identified in kernel fat of whitebark pine in order of abundance

Fatty acid	Total fatty acid methyl esters
	Percent
Linoleic	46.9
Oleic	30.6
γ-Linolenic	9.9
Palmitic	4.2
Stearic	2.7
11-Eicosenoic	1.4
γ-Linoleic	1.2
5-, 11-, 14-Eicosatrienoic	.8
11-, 14-Eicosadienoic	.7
Arachidic	.6
Linolenic	.3
Behenic	.2
Vaccenic	.1
5-, 11-Eicosadienoic	.1
Unknowns	.3
Total	100.0

Whitebark pine's protein content of 21 percent compares with pinyon pine values in the range of 10 percent (*Pinus monophylla*) to 19 percent (*P. cembroides*) (Lanner 1981); 25 percent in *P. sabiniana*, and 31 percent in *P. pinea* (Farris 1983).

The proteins in pine nuts are almost entirely seed storage proteins of the megagametophyte. Following the hydrolysis of these proteins, the component amino acids are exported into the growing points of the embryo (Lammer and Gifford 1989). Gifford (1988) has shown there is considerable variation in electrophoretic characteristics of seed proteins of several species (including *P. albicaulis*); and Schirone and others (1991) have shown such variation to have taxonomic significance. It is therefore surprising to see the almost-identical amino acid profiles of *P. pinea* and *P. edulis* seed proteins (table 2). These species are in separate subgenera of *Pinus* (Critchfield and Little 1966) and would be expected to have proteins of quite different composition.

Four common amino acids were missing from whitebark pine seed protein. Hydroxyproline's absence can probably be attributed to a lack of that amino acid in embryo and storage protein, and its restriction to seed coats and pericarp material (Van Etten and others 1967). Tryptophan is generally a minor component of plant proteins (White and others 1959) and can be destroyed in analysis (Farris 1983). Neither cystine nor cysteine were identified in whitebark pine, though the former is found in small quantities in *P. edulis* and *P. pinea* (table 2). The lack of cystine and the low quantity of methionine indicate that sulfur-containing amino acids are of little importance to development of whitebark pine seedlings.

Perhaps the most striking difference between seed protein of whitebark pine and the other species in table 2 is its great abundance of lysine. Lysine, an essential amino acid for human growth, is notoriously low in cultivated members of the Graminae. Feeding experiments conducted with dark-eyed juncos (*Junco hyemalis*) by Parrish and Martin (1977)

have established the essentiality of lysine in maintaining a positive nitrogen balance in that bird. Additional amino acids found essential for poultry are arginine, glycine, and histidine, all of which are found in whitebark pine nuts (table 1). In the absence of data specific to the genus *Nucifraga*, we speculate that these nuts contain all the amino acids essential to nutcrackers.

According to Van Etten and others (1967) the nutritionally essential amino acid requirements for swine are similar to those of humans. If the requirements for bears are also reasonably similar, then whitebark pine protein, as well as its fat, may be of great dietary significance for bears. Bears are more likely to satisfy their protein needs from a wider variety of foodstuffs than nutcrackers, however.

The fat content of whitebark pine nuts in this study (52 percent) is quite similar to that of other stone pines as determined by Tikhomirov (1939): *P. cembra*, 59.9 percent and *P. pumila*, 59.4 percent. Fat values for *P. sibirica* vary over the range 51 to 75 percent (Shimanyuk 1963). The fat content of pinyon pines (Lanner 1981) ranges from 23 percent in *P. monophylla* to 62 to 71 percent in *P. edulis*. Farris (1983) reports that *P. sabiniana* kernels contain 49 percent of fat, and *P. pinea* contains 47 percent.

Tikhomirov (1939) reported the fat content of *P. koraiensis* to be 52.5 percent, but recent work by Yoon and others (1989) reports a crude lipid fraction of 72.5 percent, which reduced to 70.4 percent when purified.

The most notable features of the whitebark pine seed's fatty acids are the preponderance of oleic (30.6 percent) and linoleic (46.9 percent) acids. These are both unsaturated fatty acids, and it appears they are commonly the major ingredients of the seed fatty acids (f.a.) of *Pinus*. Thus they comprise 28.4 percent and 47.9 percent of the f.a. of *P. koraiensis*, 40.0 percent and 41.9 percent of the f.a. of *P. edulis* (R. M. Lanner, unpubl. data), and 42.5 percent and 42.0 percent of the f.a. of *P. monophylla*, respectively (R. M. Lanner, unpubl. data). According to Yoon and others (1989) the f.a. of *P. koraiensis* are 8.75 percent saturated, 29.41 percent monounsaturated, and 61.64 percent polyunsaturated. *Pinus edulis* and *P. monophylla* have over 80 percent polyunsaturates. The nut of *P. sabiniana* was found by Farris (1983) to be 50.5 percent oleic and 45.2 percent linoleic acids—over 95 percent polyunsaturated.

In addition to containing very high ratios of unsaturated to saturated fatty acids, pine nuts are also free of cholesterol (McCarthy and Matthews 1984). Yoon and others (1989) point out that *P. koraiensis* nuts have long been used in Korean medicine, and the nut oil of *P. cembra* had medicinal uses in Poland during the 17th century (Bialobok 1975). Yoon and others point out that *P. koraiensis* seeds contain omega-5 fatty acids, the functions of which in the human body are unknown. They suggest that these f.a. may be beneficial to health, and should be studied in relation to lipid and glucose metabolism.

VARIABLE DORMANCY

The variable dormancy that characterizes whitebark pine seeds has been viewed as a bothersome habit that makes the nurseryman's task more difficult. However, it could well be a trait that has an important biological function and that has been naturally selected to perform that

Table 4—Number of years during a 15-year period in which seeds will be germinating, under assumptions of different seed-crop intervals, and of dormancy varying from 0 to 3 years¹

Period of seed dormancy	Interval between successive seed crops														
	Years														
—	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
0	15	8	5	4	3	3	3	2	2	2	2	2	2	2	1
1	15	15	10	8	6	6	5	4	4	4	4	4	4	3	2
2	15	15	15	12	9	9	7	6	6	6	6	6	5	4	3
3	15	15	15	15	12	11	9	8	8	8	8	7	6	5	4

¹Seeds dormant for 0 years all germinate the spring following dispersal. Seeds dormant more than 0 years germinate in part in the spring following dispersal; and in part during each additional spring for 1, 2, or 3 years.

function. Here we postulate and examine several possible evolutionary functions for variable dormancy.

Increased Fitness

According to this hypothesis, the conditions met by germinating seeds may vary greatly from year to year. Therefore a cohort of seeds dispersed in fall of the year n may be confronted by disadvantageous—or even catastrophic—conditions in spring of $n+1$. Such conditions could result from severe frost or drought (Kozlowski and Gunn 1972). If so, it might be to the plant's advantage to delay germination of some seeds until spring of $n+2$ or even $n+3$ or beyond. If the temporal spacing of seed crops and the lengths of the variable dormancy periods are matched properly, partial seed cohorts could be germinating nearly every year. Under such a scenario there would be a high probability of some seeds germinating during the years of most favorable conditions.

As an example, assume a pine stand bearing seeds in the first year of an arbitrarily chosen 15-year period. If seed crops reoccur every 4 years (in years 5, 9, and 13 of this 15-year period), and if germination occurs only in the spring following dispersal (spring of years 2, 6, 10, and 14), then there will be 4 years during the 15-year period when seedlings can become established (table 4). However, if some of those seeds remain dormant for variable lengths of time, germinating not only in the spring following dispersal, but in the next three springs as well, seedlings can become established during all 15 years of the period (table 4). Even if seed crops were spaced at 10-year intervals, this level of variable dormancy would produce seedlings in 8 of the 15 years. Thus it is apparent that variable dormancy can neutralize the effects of infrequent crop years by creating a steady stream of germinating seeds during and between crop years.

If variable dormancy increases whitebark pine's fitness by increasing the frequency of germination years, one might expect associated conifers—especially other pines—to show the same dormancy behavior. Apparently, however, this seems not to be the case. If we assume that stratification treatments prescribed to overcome seed dormancy are an index of a seed's behavior in nature, it is apparent that the subalpine conifers of western North America show no consistency (table 5). This does not mean that whitebark pine derives no benefits from being able to provide germinants in most

years, but perhaps that **only** whitebark pine (and maybe *P. monticola*) enjoys those benefits. Apparently variable dormancy is not a requirement for success of whitebark pine's associates in the subalpine zone. In fact, variable dormancy might be detrimental to these other conifers, because, except for *P. flexilis*, they have wind-dispersed seeds that lie on the soil surface, where they are vulnerable to predation. Buried seeds of whitebark pine (and limber pine) would be more likely to survive an additional year or more of "waiting" to germinate.

If variable dormancy is a genetically controlled character, it would be important to learn its mode of inheritance. For example, do all the seeds of a tree exhibit the same dormancy behavior, as would be expected in a maternally transmitted characteristic of seed-coat or megagametophytic tissue; or do they segregate, as would be expected if inheritance from both parents is manifested in variable embryo behavior? If the latter, is genetic control due to major gene effects, or is control achieved multigenically? Seed tests would need to be made with the products of controlled crosses to unravel this and similar questions, and careful anatomical studies would have to be made to better understand embryo growth and development.

Table 5—Recommended¹ cold stratification periods for seeds of subalpine conifers of western North America and their overlap with that of *Pinus albicaulis*

Species	Stratification period	Overlap of <i>P. albicaulis</i> stratification period
	Days	Percent
<i>Pinus albicaulis</i>	90 - 120	—
<i>P. monticola</i>	30 - 120	100
<i>P. flexilis</i>	21 - 90	3
<i>P. aristata</i>	0	0
<i>P. balfouriana</i>	90	3
<i>P. contorta</i> var. <i>latifolia</i>	30 - 56	0
<i>P. contorta</i> var. <i>murrayana</i>	20 - 30	0
<i>Tsuga mertensiana</i>	90	3
<i>Picea engelmannii</i>	0	0
<i>Abies lasiocarpa</i>	28	0
<i>A. amabilis</i>	21 - 28	0
<i>A. magnifica</i>	28 - 42	0

¹In USDA FS 1974.

Phylogenetic Legacy

Perhaps whitebark pine exhibits variable dormancy simply because the trait is common to a group of related species that includes whitebark pine. To determine this, we have displayed in table 6 the available stratification requirements of pines of *Pinus* subg. *Strobos* by subsection.

Species characterized (in USDA FS 1974) as "suspected of having immature embryos at the time of collection" or of exhibiting "extreme dormancy" are identified by superscript numbers. The densest concentration of superscripts is in the stone pines—subsection *Cembrae*—in which all species require more than 60 days of stratification to germinate (table 6). Thus it seems likely that variable dormancy is not just an *albicaulis* trait, nor a broad *Strobos* trait, but a subsection *Cembrae* trait. This is consistent with my earlier suggestion (Lanner 1980) that the *Cembrae* pines are of monophyletic origin.

Nutcracker Retention

The importance of variable dormancy may lie in its effects on whitebark pine's seed disperser, Clark's nutcracker. Whitebark pine depends on the nutcracker for seed dispersal and seedling establishment (Hutchins and Lanner 1982), so it is in the long-term interest of the pine to retain nutcracker populations in its ecosystem. We suggest that variable dormancy can have that effect.

The following scenario illustrates our argument. A mast year occurs in whitebark pine (year n). The local nutcracker population frantically harvests and caches several times as many seeds as are required to ensure its own survival and that of its offspring until the next fall (Hutchins and Lanner 1982; Tomback 1978; Vander Wall and Balda 1977). Throughout the fall, the nutcrackers recache their buried seeds (Hutchins and Lanner 1982). The next summer, in year $n+1$, some seeds germinate. The birds now have three sources of food—their own caches, from which they continue to feed; the seeds now germinating and therefore visible; and the still-dormant seeds from the same caches, whose locations are betrayed by the $n+1$ germinants (Vander Wall and Hutchins 1983). Each bird now knows not only the locations of all its own caches, but also the caches made by other birds in which $n+1$ germinants were found. Even if there is no crop in the second year, the bird's 9-month memory (Balda 1992) of cache location will allow it to survive until the third year, when a new crop may be present. Again, sprouting seeds of $n+2$ will betray the locations of remaining caches. If there is again no crop, or only a light one, the nutcrackers may be able to survive by recaching the dormant seeds they have found associated with germinating seeds. This assumes that another 9-month period of cache remembrance follows each caching event. Due to the overlapping of periods of availability of current-crop seeds and seeds of the previous crop still lying dormant up to 3 years in caches, plus those germinating, nutcrackers should be able to remain in situ except in years following several successive crop failures.

Such a scenario could not occur with seeds that all sprouted in $n+1$. With variable dormancy it appears to be a strong possibility; however, intensive observation and additional data will be required to determine whether it

Table 6—Recommended¹ cold stratification periods for seed of some pines in subgenus *Strobos*, and their overlap with that of *Pinus albicaulis*

Species	Stratification period	Overlap of <i>P. albicaulis</i> stratification period
	Days	Percent
(<i>Pinus</i>) <i>albicaulis</i> ²	90 - 120	—
subsection <i>Strobi</i>		
<i>flexilis</i> ²	21 - 90	3
<i>monticola</i> ²	30 - 120	100
<i>strobos</i>	60	0
<i>strobiformis</i> ²	60 - 120	100
<i>lambertiana</i> ²	60 - 90	3
<i>peuce</i>	0 - 60	0
<i>parviflora</i> ^{2,3}	90	3
<i>griffithii</i>	0 - 15	0
subsection <i>Balfourianae</i>		
<i>aristata</i>	0	0
<i>balfouriana</i> ²	90	3
subsection <i>Cembroides</i>		
<i>cembroides</i>	0	0
<i>edulis</i>	0	0
<i>monophylla</i> ²	28 - 90	3
<i>quadrifolia</i>	0	0
subsection <i>Cembrae</i>		
<i>cembra</i> ^{2,3}	90 - 270	100
<i>sibirica</i> ^{2,3}	60 - 90	3
<i>pumila</i> ²	120 - 150	3
<i>koraiensis</i> ^{2,3}	90	3

¹In USDA FS 1974.

²Characterized as exhibiting "extreme dormancy" (requiring more than 60 days of stratification in USDA FS 1974).

³Characterized as "suspected of having immature embryos at the time of collection" in USDA FS 1974.

is realistic. Our intention in speculating is to stimulate further study of this possibility. All of this illustrates that to understand whitebark pine's variable seed dormancy, the nutcracker too must be considered. As pointed out by Lanner (1980): "The ecology and evolution of the wingless-seeded 'Bird Pines' can only be understood in a frame of reference that includes the behavior of their feathered dispersers." The bare facts of the mutualism of whitebark pine and Clark's nutcracker are by now well established. The time is ripe to study the complexities of the relationship, and its second-order effects.

REFERENCES

- Balda, R. P. 1992. [Conversation with Ronald M. Lanner]. August 14. Flagstaff, AZ: Northern Arizona University.
- Bialobok, S., ed. 1975. Stone-pine (*Pinus cembra* L.). Translated from Polish for U.S. Department of Agriculture and National Science Foundation. National Technical Information Service TT-73-54045. 173 p.
- Critchfield, W. B.; Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991.

- Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Farris, G. J. 1983. California pignolia: seeds of *Pinus sabiniana*. *Economic Botany*. 37: 201-206.
- Gifford, D. J. 1988. An electrophoretic analysis of the seed proteins from *Pinus monticola* and eight other species of pine. *Canadian Journal of Botany*. 66: 1808-1812.
- Hubbard, W. D. 1977. Comparison of various methods for the extraction of total lipids, fatty acids, cholesterol, and other sterols from food products. *Journal of the American Oil Chemists' Society*. 54: 81-83.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Kendall, K. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. In: Meslaw, Charles E., ed. *Bears—their biology and management*. West Glacier, MT: International Association for Bear Research and Management: 166-173.
- Kozłowski, T. T.; Gunn, C. R. 1972. Importance and characteristics of seeds. In: Kozłowski, T. T., ed. *Seed biology*. New York: Academic Press: 1-20.
- Lammer, D. L.; Gifford, D. J. 1989. Lodgepole pine seed germination. II. The seed proteins and their mobilization in the megagametophyte and embryonic axis. *Canadian Journal of Botany*. 67: 2544-2551.
- Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Dancik, B. P.; Higginbotham, K. O., eds. *Sixth North American forest biology workshop proceedings; 1980 August 11-13; Edmonton, AB*. Edmonton, AB: University of Alberta: 15-45.
- Lanner, R. M. 1981. The piñon pine: a natural and cultural history. Reno, NV: University of Nevada Press. 208 p.
- Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. *Canadian Journal of Forest Research*. 12: 391-402.
- Mattson, D. J.; Jonkel, C. 1990. Stone pines and bears. In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology of a high-mountain resource; 1989 March 29-31; Bozeman, MT*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 223-236.
- McCarthy, M. A.; Matthews, R. H. 1984. Composition of foods: nut and seed products. *Agric. Handb.* 8-12. Washington, DC: U.S. Department of Agriculture, Human Nutrition Information Service. 137 p.
- McCaughey, W. 1992. [Letter to Ronald M. Lanner]. February 25. 1 leaf. Bozeman, MT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Parrish, J. W., Jr.; Martin, E. W. 1977. The effect of dietary lysine level on the energy and nitrogen balance of the dark-eyed junco. *Condor*. 79: 24-30.
- Pitel, J. A.; Wang, B. S. P. 1990. Physical and chemical treatments to improve germination of whitebark pine seeds. In: Schmidt, W. C.; McDonald, K. J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology of a high-mountain resource; 1989 March 29-31; Bozeman, MT*. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 130-133.
- Schirone, B.; Piovesan, B.; Bellarosa, R.; Pelosi, C. 1991. A taxonomic analysis of seed proteins in *Pinus* spp. (Pinaceae). *Plant Systematics and Evolution*. 178: 43-53.
- Shimanyuk, A. P., ed. 1963. *Fruiting of the Siberian stone pine in east Siberia*. Translated from Russian for U.S. Department of Agricultural and National Science Foundation by Israel Program for Scientific Translations. Jerusalem. 204 p.
- Tikhomirov, B. A. 1939. Khozyaistvenoye ispol'zovaniye kedrovogo stlannika. *Sov. Sever*. 4: 62-65.
- Tombach, D. F. 1978. Foraging strategies of Clark's nutcracker. *Living Bird*. 16: 123-161.
- Turcek, F. J.; Kelso, L. 1968. Ecological aspects of food transportation and storage in the Corvidae. *Communications in Behavioral Biology Part A*. 1: 277-297.
- U.S. Department of Agriculture, Forest Service. 1974. *Seeds of woody plants in the United States*. *Agric. Handb.* 450. Washington, DC: U.S. Department of Agriculture, Forest Service. 883 p.
- Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs*. 47: 89-111.
- Vander Wall, S. B.; Hutchins, H. E. 1983. Dependence of Clark's nutcracker, *Nucifraga columbiana*, on conifer seeds during the postfledging period. *Canadian Field Naturalist*. 97: 208-214.
- Van Etten, C. H.; Kwolek, W. F.; Peters, J. E.; Barclay, A. S. 1967. Plant seeds as protein sources for food or feed. Evaluation based on amino acid composition of 379 species. *Journal of Agricultural and Food Chemistry*. 15: 1077-1089.
- White, A.; Handler, P.; Smith, E. L.; Stetten, D. 1959. *Principles of biochemistry*. New York: McGraw-Hill Book Co. 1149 p.
- Yoon, T.-H.; Im, K.-J.; Koh, E. T.; Ju, J.-S. 1989. Fatty acid compositions of *Pinus koraiensis* seed. *Nutrition Research*. 9: 357-361.

BEAR USE OF WHITEBARK PINE SEEDS IN NORTH AMERICA

David J. Mattson
Daniel P. Reinhart

Abstract—Whitebark pine (*Pinus albicaulis*) seeds are an important high-quality food for bear populations that occupy ecosystems with continental climates south of the United States-Canada border. Availability of pine seeds affects levels of human-bear conflict and bear mortality. In most areas bears acquire whitebark pine seeds by excavating red squirrel (*Tamiasciurus hudsonicus*) food caches. Squirrel densities appear to limit bear use of pine seeds more than abundance of whitebark pine. Thus management of whitebark pine habitats for bear use primarily involves management to favor red squirrels. Bear use of pine seeds is restricted to stands >100 years old, and can persist for an additional 200 to 300 years. Consequently stand rotations of 300 years and harvest rates of 3 percent per decade are recommended. Also, because of potential or demonstrated negative impacts associated with global climate change and white pine blister rust (*Cronartium ribicola*), long-term prospects for whitebark pine should be part of considerations when managing habitats of bear populations, especially insular populations.

Whitebark pine seeds are a predictably high-quality bear food given their relatively large size, high fat content, and moderately high digestibility (table 1). Fat content is perhaps the most important attribute of these seeds, given the importance of body fat to the life strategy of bears (Stirling and Derocher 1990) and the greater efficiencies of body fat accumulation associated with high dietary fat content (Hadley 1985; Schemmel 1976). On the other hand, use of whitebark pine seeds especially by grizzly bears (*Ursus arctos horribilis*) is complicated by the indehiscent nature of whitebark pine cones (Lanner 1990), and the consequent reliance of most bears on windthrow or rodent intermediaries for access to the seeds (Kendall 1983; Mattson and Jonkel 1990; Taylor 1964).

Black (*Ursus americanus*) and grizzly bears have probably made use of pine seeds for as long as these two species have coexisted with whitebark pine, approximately 2 million years for black bears and 12,000 years for grizzly bears (Axelrod 1986; Kurten and Anderson 1980). Although aboriginal Americans were probably aware of this relationship, the first written records of bears using whitebark pine seeds did not appear until well into the

20th century, in articles by authors such as Cahalane (1947), Taylor (1964), and Tisch (1961). Details of the relationship between bears and whitebark pine seeds have only recently been published, focusing on interior areas characterized by more continental climates (Craighead and others 1982; Kendall 1983; Mattson and Jonkel 1990; Mattson and others 1992, 1993). In this paper we update information presented by Mattson and Jonkel (1990), and further elaborate on some aspects of the relationship between bears and whitebark pine in North America.

PATTERNS OF BEAR USE

Geographic Distribution

Bears consistently make use of whitebark pine seeds only south of the United States-Canada border, where whitebark pine is a potentially abundant component of subalpine forests (fig. 1). However, even in this area major differences in intensity of bear use are evident, associated with maritime and continental climates.

We examined published bear food habits studies from western North America that included the results of 13,130 bear feces examinations. Our analysis clearly showed that the consistency and relative frequency of whitebark pine seed use was much greater (18.7 percent) in areas

Table 1—Size, nutrient content, and relative digestibility by ursids of whitebark pine seeds; compiled from Craighead and others (1982), Kendall (1983), Lanner and Gilbert (these proceedings), Mealey (1975), Pritchard and Robbins (1990), Weaver and Forcella (1986), and unpublished Interagency Grizzly Bear Study Team data

Parameters	Range of means	Mean among studies	Range of standard deviations
Seeds per cone	75-88	80	26-28
Dry seed weight (g)	0.07-0.10	0.09	0.01-0.02
Percent protein content ¹	11.9-14.2	12.8	
Percent ether extract ¹	21.8-30.4	27.1	
Percent nitrogen-free extract ¹	12.4-27.2	19.8	
Percent crude fiber ¹	34.8	(34.8)	
Percent total dietary fiber ^{1,2}	40.3	(40.3)	
Percent digestible energy	³ 50.1/ ⁴ 48.7	49.4	³ 1.4

¹Based on whole seed dry weight.

²Calculated for pinyon pine (*Pinus edulis*) seeds.

³Calculated based on laboratory feeding trials (Pritchard and Robbins 1990).

⁴Calculated from differential between field samples of fresh whole material and feces (Mealey 1975).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

David J. Mattson is Wildlife Biologist, Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717; Daniel P. Reinhart is Management Biologist, National Park Service, Resource Management, Yellowstone National Park, WY 82190.



Figure 1—Distribution of whitebark pine and use of whitebark pine seeds by bears in North America. Sparser Canadian distribution of whitebark pine is indicated by dotted lines. Three different levels of pine seed use (<1 percent, 1-10 percent, and >10 percent frequency in bear feces) are also indicated.

with continental climates compared to areas with maritime climates (2.7 percent) or areas in Canada where whitebark pine was sparse (2.8 percent) ($df = 2$, $G = 987.3$, $P < 0.001$).

These differences are logically attributable to several factors. In areas where whitebark pine is scarce, the bears may not consider it to be a food, or not choose to use its seeds if they are disjunct from other higher value feeding opportunities. Areas influenced by maritime climates are characterized by an abundance of berry-producing shrubs, typically at elevations much lower than whitebark pine (Jonkel and Cowan 1971; Poelker and Hartwell 1973; Servheen 1983; Tisch 1961; and others). These berries are probably more valuable than whitebark pine seeds, and so local bears would logically tend to use berry-rich habitats to the exclusion of whitebark pine habitats (Tisch 1961). Conversely, in areas with continental climates berries are typically fewer and whitebark pine more abundant (Aune and Kasworm 1989; Mattson and others 1991). We hypothesize that for this reason bears would logically focus more on the consumption of whitebark pine seeds. Recent heavy whitebark pine mortality in maritime areas, caused by white pine blister rust, has also arguably had negative effects on bear use of pine seeds in these areas (Kendall and Arno 1990; Mattson and Jonkel 1990).

Because the large majority of whitebark pine seed use by bears has occurred in interior ecosystems, our subsequent discussion will focus on these areas; and because most research concerning bear use of pine seeds comes from the Yellowstone ecosystem, most of the results presented here are from this study area.

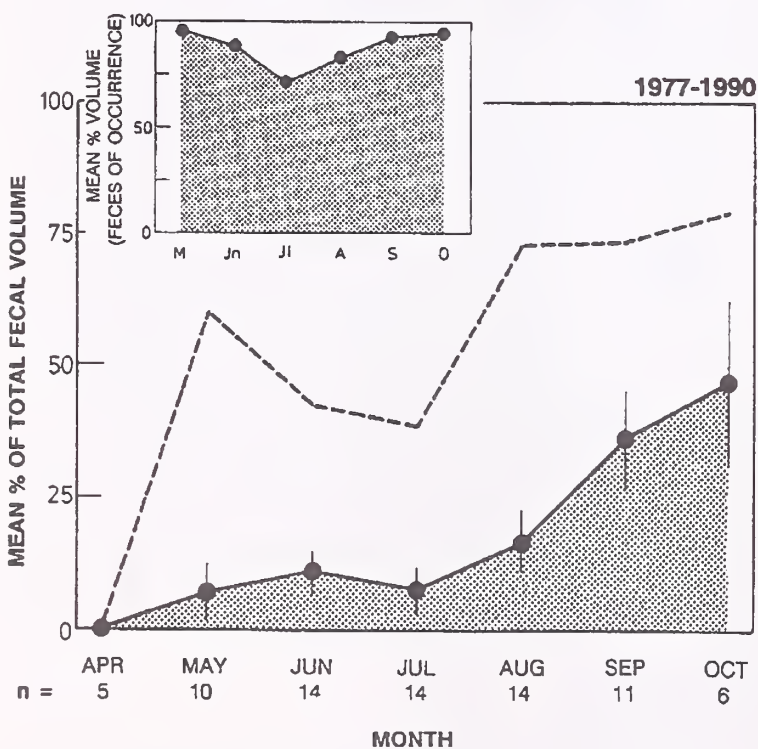


Figure 2—Mean percent volume of pine seeds in Yellowstone grizzly bear feces by month, 1977-90. Maximum recorded volume is indicated by dashed lines and mean percent volume of pine seeds in feces of occurrence is shown in the inset.

Temporal Variation in Use

Seasonal Variation—Because whitebark pine seeds are durable, bears use not only seeds contemporary to their maturation, but also seeds that survive for up to 1 year after initial availability of a large crop (Kendall 1983; Mattson and Jonkel 1990; Mattson and others 1993). Current-year use usually begins after mid-August with onset of caching by red squirrels (Hutchins and Lanner 1982), but can vary from late July to early September, apparently depending on seed maturation (Mattson and others 1993). Use of overwintered seeds does not usually begin until after mid-May (Mattson and Jonkel 1990), but can begin as early as the first week of April and involve excavation of cones out of squirrel middens, through snow 0.3-1.2 m deep (Kendall 1983).

Use of both current-year's and overwintered seeds by bears results in a primary September-October peak and a secondary June peak in frequency of pine seeds in bear feces, when averaged over a number of years (fig. 2). With the exception of July, bear feces tend to consist almost exclusively of pine seed remains (>80 percent) when bears are in the whitebark pine zone feeding on pine seeds (fig. 2).

Annual Variation—Use of pine seeds by bears varies considerably among years. In the Yellowstone area, pine seeds have dominated the diet during some years (for example 1979) and been virtually absent other years (for example 1977, 1982, and 1988) (Mattson and others 1991, 1992). This variation in use is related to seed crop size, with heavy use occurring only when crops average >13-23 cones per tree (from counts on permanent transects), approaching an asymptote of use (75 percent frequency in feces) at crop sizes averaging 38 cones per tree. Use of overwintered pine seeds during the following June-July is similarly related to crop size, but with inflection points of 20-29 seeds and an asymptote of 38 percent frequency in feces (fig. 3). This relationship between bear use and crop size is acutely sigmoidal, suggesting the existence of a use threshold that is possibly related to saturation of demand by competing birds and rodents, nonlinear increases in foraging efficiency, or both. The higher thresholds and lower asymptote associated with use of overwintered seeds is attributable to depletion of the crop during the previous fall and winter.

Varying inflection points in the hypothesized relationship between bear use and seed crop size reflect an apparent trend over the years 1980-91 toward lower thresholds to substantial bear use (fig. 3). The years 1980 and 1981 are further distinguished by the relative insensitivity of bear use to crop size compared to later years. Interestingly, asymptotes associated with maximum potential bear use have not varied significantly during this same time period. At the very least, this variance suggests that the relative intensity with which bears use pine seeds in a given study area can change. The causes of these apparent changes can only be speculated, including: increasingly efficient use of comparable-sized crops by the Yellowstone bear population; and an increasing willingness to use seeds under less optimal conditions, attributable either to increasing bear densities or decreasing overall carrying capacity.

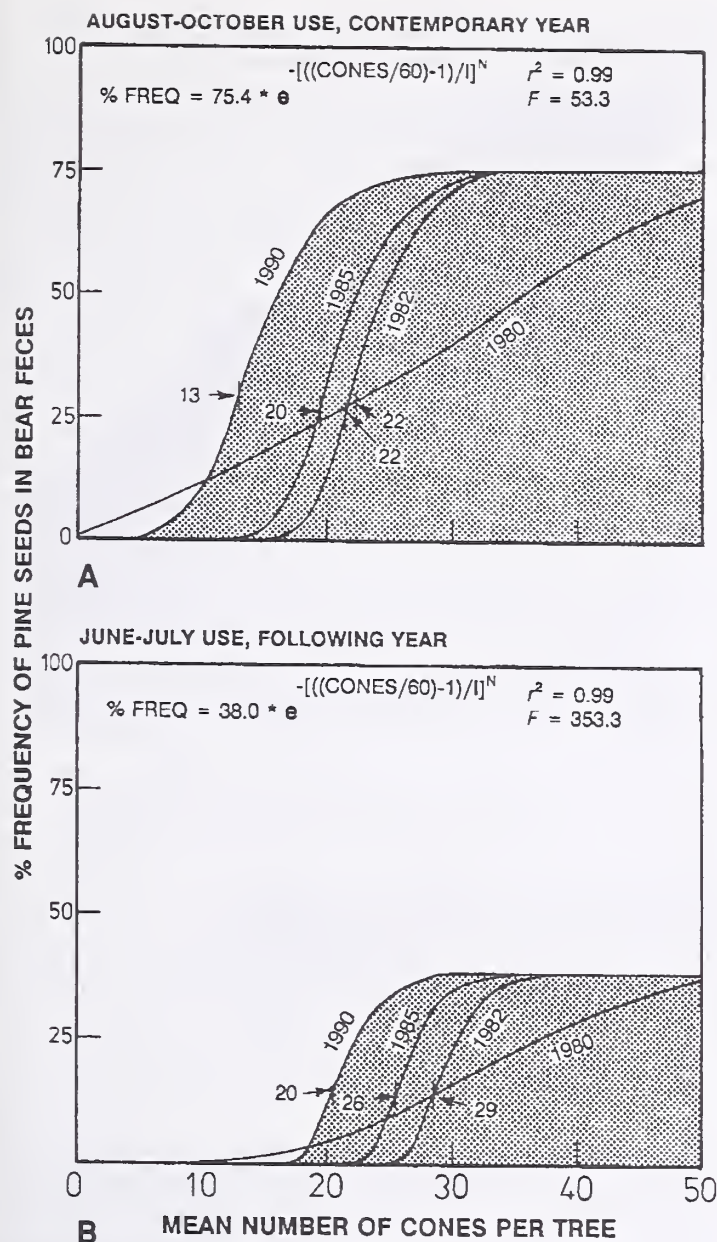


Figure 3—A, relationship between frequency of whitebark pine seeds in August-October Yellowstone grizzly bear feces and mean number of cones counted per tree on permanent transects during the contemporary year, 1980-91. B, relationship between frequency of pine seeds in June-July feces and mean number of cones counted the previous fall, 1980-91.

Interestingly, in a part of Montana characterized by a more maritime climate and relatively little bear use of pine seeds, Tisch (1961) counted an average of five and 16 cones per tree during 1959 and 1960, respectively. Both of these averages were less than the approximately 20 cones per tree associated with the onset of heavy pine seed use in the Yellowstone area.

Habitats Associated With Use

Elevation and Aspect—As would be expected, bear use of whitebark pine seeds is restricted to elevations above the lower limits of whitebark pine distribution. This lower elevational limit varies with latitude and longitude, from about 2,400 m in the Yellowstone area

(44.5° N.) to 1,890 m along the East Front of the Montana Rockies (47.5° N.) (Mattson and Jonkel 1990).

However, within this constraint bear use varies considerably among aspects and elevations, depending on the year. We found that during three successive large seed crops in the Yellowstone area, bear use was nonrepetitive among broad aspectual and elevational categories; during 1985-86 heaviest on east aspects at mid-elevations, during 1987 heaviest on west and north aspects at low- to mid-elevations, and during 1989-90 heaviest on east and south aspects at high elevations (Mattson and others 1993). We also found differences in elevational distribution of pine seed use between two successive crops at a local scale, in the Cooke City area northeast of Yellowstone National Park, with use concentrated at elevations >2,870 m during 1990 and at elevations <2,720 m during 1991 (Reinhart and Mattson 1992). This geographic variation was inconclusively related to seed production, but demonstrated the potential for considerable differences in habitat distribution of pine seed use over a 6- to 7-year period.

Habitat Types—Ecosystems in the Western United States have been described in terms of ecological landscape units called habitat types, that are further aggregated as series and split into phases (Pfister and others 1977; Steele and others 1983). In the Yellowstone area most bear use of pine seeds has occurred with varying intensity in 14 different habitat types. In accord with variation in distribution of pine seed use among aspects and elevations, distribution of pine seed use by bears has also varied among habitat types (Mattson and others 1993). Even so, the *Abies lasiocarpa* / *Vaccinium scoparium* - *Pinus albicaulis* phase, and the *Abies lasiocarpa* / *Calamagrostis canadensis* and *Abies lasiocarpa* / *Thalictrum occidentale* habitat types have been used intensively during all years when pine seeds are abundant (Mattson and Jonkel 1990). Conversely, use of habitat types at lowest and highest elevations of the whitebark pine zone has been most varied. Habitats in interior ecosystems where whitebark pine is a climax overstory species have been only rarely used by bears for foraging on pine seeds (Mattson and Jonkel 1990). However, even in these habitats heavy use can occur, as during 1989-90 in the Yellowstone area (Mattson and others 1993).

Distribution of pine seed use among habitat types was surprisingly consistent between study areas in the Yellowstone ecosystem and along the East Front of the Montana Rocky Mountains (Mattson and Jonkel 1990). This suggests that patterns of habitat use associated with bear consumption of pine seeds are consistent among areas with continental climates, and that more detailed results pertaining to habitat use from the Yellowstone ecosystem are extrapolable over interior regions of the United States. Because very little information is available concerning bear use of pine seeds in more maritime ecosystems, we can make no inferences about patterns of use in these areas other than it being restricted to sites with mature cone-producing whitebark pine.

Red Squirrel and Whitebark Pine Abundance—Red squirrel density is probably the most important proximal factor affecting bear use of pine seeds in interior ecosystems. The importance of red squirrels to especially

grizzly bear foraging has been observed by Kendall (1983), Mattson and Jonkel (1990), and Schallenberg and Jonkel (1980). Craighead and others (1982), Graber and White (1983), Murie (1944), and Raine and Kansas (1990) also mentioned rodent or squirrel caches as potential sources of pine seeds for bears, but were more equivocal about the overall importance of these intermediaries. Interestingly, neither Craighead and Craighead (1972) nor Mealey (1975) mention that grizzly bears raided red squirrel food caches during their studies in Yellowstone. The disparity between these and later observations in the Yellowstone area is not easily reconciled, and suggests that differences could be at least partly attributable to variation in bear behavior and pine seed availability described earlier.

Most (86 percent) of 232 sites where grizzly bears were known to have used pine seeds in the Yellowstone area, 1986-91, involved bears excavating red squirrel cone caches. All but five of the other 32 instances where grizzly acquired pine seeds by scavenging fallen cones occurred during 1989-90 when much of the cone production occurred at elevations above the normal range of red squirrels (Mattson and others 1993; Reinhart and Mattson 1990). Conversely, 51 percent of 53 sites where black and grizzly bears used pine seeds near Cooke City, MT, during 1990-91 were characterized by scavenging of fallen cones (Reinhart and Mattson 1992). This observation suggests that scavenging of fallen cones can be locally important. However, all 26 instances when bears scavenged fallen cones in this area occurred during 1990, in conjunction with use of seeds overwintered from the unusually high-elevation crop of 1989.

Scavenging apparently predominates over excavation of squirrel caches in environments where squirrels are rare. Red squirrel densities in the whitebark pine zone are strongly related to a site favorability index ($r^2 = 0.79$), with squirrel densities increasing as exposure to prevailing winds and elevation decreases (Reinhart and Mattson 1990). Given that basal area and exclusivity of whitebark pine increase with wind exposure and elevation (Mattson and Reinhart 1990), there is an inherently negative relationship between dominance of whitebark pine and density of red squirrels within the whitebark pine zone. Thus, scavenging predominates over midden excavation where whitebark pine comprises >75 percent of the overstory (four categories of whitebark pine percentage; $df = 3$, $G = 69.7$, $P < 0.001$), and at elevations >2,870 m (four elevation categories; $df = 3$, $G = 42.4$, $P < 0.001$); where red squirrels are rare.

Bear use of pine seeds is clearly the result of opportunities implicit to the varying abundance of red squirrels and whitebark pine. However, there is reason to hypothesize that squirrel densities impose greater constraints on bear use of pine seeds than does abundance of whitebark pine. We analyzed data from 1987 to examine this hypothesis, looking at the relationship between unit area volume of excavations for pine seeds by Yellowstone grizzly bears and red squirrel density and whitebark pine basal area (fig. 4). At any given squirrel density, bear use abruptly increased and approached maximum levels at relatively low basal areas of whitebark pine, between approximately 3 and 8 m^2/ha . Conversely, the relationship between bear activity and red squirrel densities was more nearly linear,

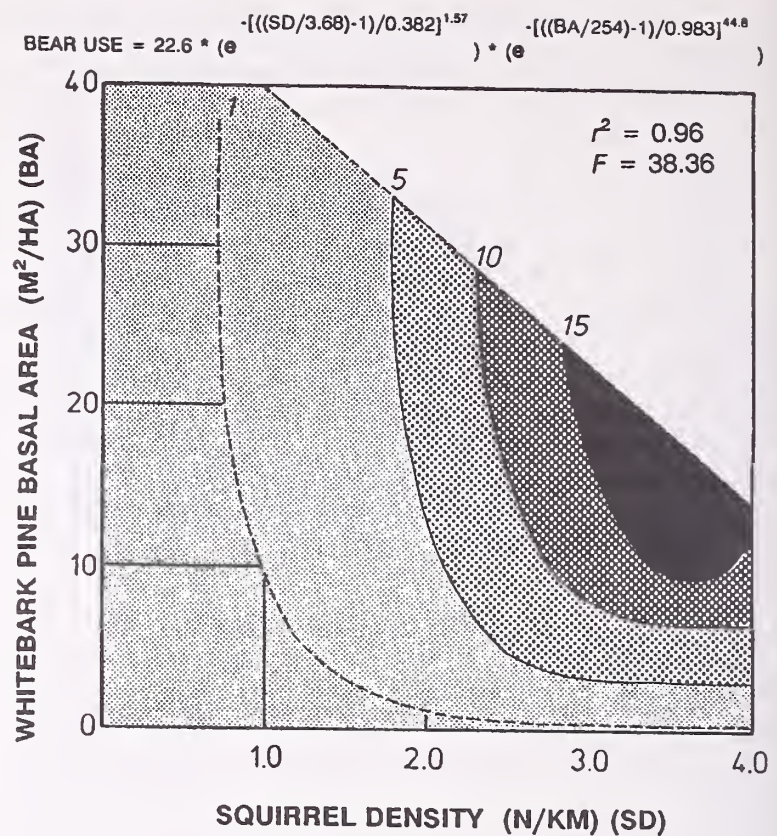


Figure 3—The relationship between intensity of grizzly bear feeding on pine seeds, as indicated by density of excavations (m^3/km) and squirrel density and whitebark pine basal area, Yellowstone area, 1987.

with excavations gradually increasing to a maximum that corresponded to maximum squirrel densities observed in the whitebark pine zone. Basically, whitebark pine basal area seemed to be associated primarily with the probability that a given midden would be excavated, sometimes repeatedly, by bears (Mattson and Reinhart 1987), with the greatest effects at very low whitebark pine abundance. Once this low threshold of whitebark pine abundance was exceeded (> about 4.3 m^2/ha), red squirrel densities appeared to limit bear use of pine seeds during most years.

Timber Stand Age—Bear use of whitebark pine seeds in the Yellowstone area has occurred almost exclusively in mature stands. According to a successional classification of timber types by Despain (1990), all bear use of pine seeds from squirrel middens and most bear use of scavenged seeds has occurred in "mature" cover types, typically designated LP2, LP3, SF, WB2, WB3, WB, or DF3. Results from a use-availability analysis of cover types in Yellowstone National Park corroborate the affinity of grizzly bears for later successional cover types when using pine seeds (Knight and others 1984). This analysis showed that the early successional WB1 cover type was consistently under-used or used without preference during all seasons, whereas mature WB cover types were consistently used with disproportionately greater intensity than expected, especially during the fall, primarily for the consumption of pine seeds.

Based on ages given by Despain (1990) cover types associated with pine seed use are rarely less than 100 years old. Ages of 160 stands in two intensive Yellowstone study areas located in the whitebark pine zone (Mattson and Reinhart 1987) also revealed that none of these mature cover types was <125 years old.

These minimum stand ages correspond with use expected by levels of cone production. Weaver and others (1990) observed that whitebark pine cone production was relatively low in stands <100 years old and reached peak levels soon thereafter. Morgan and Bunting (in press) also observed that younger WB0 and WB1 stands produced few cones and had few excellent crops. Both of these authors observed that cone production persisted at least at moderate levels in much older stands, up to 300 to 400 years old. These observations correspond well with the results of more exhaustive studies of the closely related Siberian stone pine (*Pinus sibirica*) (Axelrod 1986) by Russian researchers (Mattson and Jonkel 1990).

These relationships of use to stand age have several implications. First, potential productivity of whitebark pine sites, at least for bears, is not realized until after approximately 100 years, and can persist for 200 to 300 years thereafter. Thus, in contrast to many other temperate ecosystems where production of bear foods is concentrated on berry-producing shrubs in early successional stages, production of bear foods in the whitebark pine zone is concentrated in much older mid- to late-successional stands (Mattson 1990). Second, given these time frames, long-term productivity of the whitebark pine zone in interior ecosystems would be best assured by disturbance regimes that replaced approximately 3 percent of mature acreage per decade.

EFFECTS ON BEAR DEMOGRAPHY

Fecundity

Whitebark pine seeds are an important source of energy for bears that live in interior ecosystems of the United States. Craighead and others (1982) estimated that pine seeds were the most important source of energy for grizzly bears in their study area located east of the Continental Divide in the Rocky Mountains of Montana. Preliminary estimates by Servheen and others (1986) suggested that Yellowstone grizzly bears derived about 23 percent of their net digested energy from whitebark pine seeds, second only to the approximately 30 percent that they derived from ungulate meat. In addition, preliminary analysis of Yellowstone data suggests that female grizzly bears make proportionately much greater use of pine seeds compared to males. Thus there is a good basis for hypothesizing that availability and use of pine seeds affects the fecundity of female bears residing in these ecosystems.

Further preliminary analyses of data from the Yellowstone ecosystem offer support for this hypothesis. Female grizzly bears that frequently used whitebark pine seeds appeared to exhibit substantially higher reproductive rates and reproduce at a significantly earlier age than females who consumed few pine seeds. Much of the difference in reproductive rate, as measured by both production

and survival of offspring to weaning, was attributable to low survivorship of cubs dependent on dams that made little use of pine seeds.

Mortality and Movements

Whitebark pine seed availability has even greater effects on survivorship of subadult males and adult females than on fecundity of reproducing females. During years when pine seeds are used very little, conflicts with humans escalate dramatically in the Yellowstone area. Management-related trappings of grizzly bears instituted to alleviate these conflicts are, on average, six times as numerous during nonuse compared to use years (Mattson and others 1992). As a direct result of this increased conflict, an average of two times as many adult females and three times as many subadult males die during years when pine seeds are not available (Mattson and others 1992).

This increased mortality is not attributable to increased movement of humans among bears or to starvation, but rather to increased activity of bears around human facilities (Mattson and others 1992). Whitebark pine in the Yellowstone and Rocky Mountain East Front ecosystems tends to occur in areas remote from human facilities (Aune and Kasworm 1989; Mattson and others 1992). Thus, when bears are intensively using pine seeds they are typically far removed from humans and human-bear conflict is correspondingly low. Conversely, when pine seeds are not available bears seek out alternate foods that are often closely associated with human facilities. Historically these alternate foods were often of human origin (Knight and others 1988), but more recently these alternate foods have been natives that tend to occupy lower elevation habitats also occupied by humans (Mattson and Knight 1989). In addition, the greater movements of Yellowstone grizzly bears during years or seasons when pine seeds are not available (Blanchard and Knight 1991; Haroldson and Mattson 1985) very likely exacerbate this unfavorable situation and increase conflicts with humans.

MANAGEMENT IMPLICATIONS

Because whitebark pine seeds are apparently so important to bears in interior ecosystems of the United States, whitebark pine deserves priority in the management of bear habitat. As indicated earlier, both temporal and geographic variation in the availability of whitebark pine seeds can have major implications on the survival and fecundity of bears in these ecosystems. Thus, long-term variations in availability of pine seeds attributable to the productivity and abundance of whitebark pines warrants the concern and attention of managers.

As pointed out previously, stands with relatively little whitebark pine can be of considerable value to bears as long as they contain high densities of red squirrels. Thus, management of bear habitat for availability of pine seeds implies management to meet red squirrel habitat requirements. In the whitebark pine zone this means simultaneously maximizing stand basal area, overstory species diversity, and components of whitebark pine and Douglas-fir (*Pseudotsuga menziesii*) (Reinhart and Mattson 1990).

This kind of favorable condition often coincides with commercial forests occupying lower elevations of the whitebark pine zone; and maintenance of these conditions potentially conflicts with other management objectives related to the extraction of wood products. In areas where bear management is a high priority, timber harvest cycles should therefore employ roughly 300-year stand rotations in the whitebark pine zone, with landscape-wide harvest levels at approximately 3 percent per decade.

Global climate change has potentially major implications to the abundance of whitebark pine in interior ecosystems and consequently to the prospects of associated bear populations. Romme and Turner (1991) projected the fates of major life zones in the Yellowstone area under three different climatic scenarios likely to be associated with doubled CO₂ content in the atmosphere. Under all three scenarios they projected a decline of the whitebark pine zone to <10 percent of its current extent. Without wildfires, loss of whitebark pine may be prolonged due to the long lifespan of the species. However, increasingly frequent fires, especially under a drier scenario, could hasten the demise of whitebark pine by eliminating it from sites where it could not reestablish (Romme and Turner 1991). Thus, with global climate warming a real possibility, managers should be cautious about harvesting any whitebark pine, especially at lower elevations. In addition, judicious control of natural fires may be desirable to favor the persistence of existing mature whitebark pine.

The potential and demonstrated negative impacts of global climate change and white pine blister rust on an important source of bear food like whitebark pine point up the legitimate need for concern about long-term changes in bear habitats. This consideration is especially relevant to the management of insular bear populations, exemplified by Yellowstone's grizzly bears (Mattson and Reid 1991). In situations where occupied bear habitat is not only isolated but also restricted, bear populations are especially vulnerable to changes in carrying capacity because of limited options to shift or expand their ranges or benefit from the influx of bears from other nearby or contiguous populations. Thus, uncertainty over the long-term prospects of whitebark pine should be a major consideration in management decisions, especially those that might otherwise reduce habitat capability under the assumption of long-term habitat stability.

Finally, managers should be concerned about the placement of additional human facilities anywhere in the whitebark pine zone. Currently, most of the whitebark pine zone serves as a refuge for bears from conflict with humans, at least when pine seeds are available. This refuge effect will be diminished with every additional human intrusion. Wherever bear management is a priority, additional human facilities should not be constructed in the whitebark pine zone and existing facilities should be removed if at all possible.

REFERENCES

- Aune, Keith; Kasworm, Wayne. 1989. Final report East Front grizzly studies. Helena, MT: Montana Department of Fish, Wildlife, and Parks. 332 p.
- Axelrod, Daniel I. 1986. Cenozoic history of some western American pines. *Annals of the Missouri Botanical Garden*. 73: 565-641.
- Blanchard, Bonnie M.; Knight, Richard R. 1991. Movements of Yellowstone grizzly bears, 1975-87. *Biological Conservation*. 58: 41-67.
- Cahalane, Victor H. 1947. *Mammals of North America*. New York: Macmillan. 682 p.
- Craighead, Frank C., Jr.; Craighead, John J. 1972. Grizzly bear prehibernation and denning activities as determined by radio-tracking. *Wildlife Monograph* 32. 35 p.
- Craighead, John J.; Sumner, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. *Wildlife-Wildlands Institute Monograph* 1. Missoula, MT: University of Montana, U of M Foundation. 279 p.
- Despain, Donald G. 1990. *Yellowstone vegetation*. Boulder, CO: Roberts Reinhart. 239 p.
- Graber, David M.; White, Marshall. 1983. Black bear food habits in Yosemite National Park. In: *International Conference on Bear Research and Management: Proceedings*: 5: 1-10.
- Hadley, N. F. 1985. *The adaptive role of lipids in biological systems*. New York: John Wiley and Sons. 319 p.
- Haroldson, Mark; Mattson, David J. 1985. Response of grizzly bears to backcountry human use in Yellowstone National Park. Bozeman, MT: U.S. Department of the Interior, National Park Service, Interagency Grizzly Bear Study Team. 38 p.
- Jonkel, Charles J.; Cowan, Ian McT. 1971. The black bear in the spruce-fir forest of northwestern Montana. *Wildlife Monograph*. 27. 55 p.
- Kendall, Katherine C. 1983. Use of pine nuts by black and grizzly bears in the Yellowstone area. In: *International Conference on Bear Research and Management: Proceedings*: 5: 166-173.
- Kendall, Katherine C.; Arno, Stephen F. 1990. Whitebark pine—an important but endangered wildlife resource. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 264-273.
- Knight, R. R.; Blanchard, B. M.; Eberhardt, L. L. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973-1985. *Wildlife Society Bulletin*. 16: 121-125.
- Knight, Richard R.; Mattson, David J.; Blanchard, Bonnie M. 1984. *Movements and habitat use of the Yellowstone grizzly bear*. Bozeman, MT: U.S. Department of the Interior, National Park Service, Interagency Grizzly Bear Study Team. 177 p.
- Kurten, Bjorn; Anderson, Elaine. 1980. *Pleistocene mammals of North America*. New York: Columbia University Press. 512 p.
- Lanner, Ronald M. 1990. Biology, taxonomy, evolution, and geography of stone pines of the world. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. *Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource*; 1989 March

- 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 14-24.
- Mattson, David J. 1990. Human impacts on bear habitat use. In: International Conference on Bear Research and Management: Proceedings: 8: 33-56.
- Mattson, David J.; Blanchard, Bonnie M.; Knight, Richard R. 1991. Food habits of Yellowstone grizzly bears, 1977-1987. *Canadian Journal of Zoology*. 69: 1619-1629.
- Mattson, David J.; Blanchard, Bonnie M.; Knight, Richard R. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. *Journal of Wildlife Management*. 56(3): 432-442.
- Mattson, David J.; Jonkel, Charles. 1990. Stone pines and bears. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 223-236.
- Mattson, David J.; Knight, Richard R. 1989. Evaluation of grizzly bear habitat using habitat type and cover type classifications. In: Ferguson, Dennis E.; Morgan, Penelope; Johnson, Frederic D., comps. Proceedings—land classifications based on vegetation: applications for resource management; 1987 November 17-19; Moscow, ID. Gen. Tech. Rep. INT-257. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 135-143.
- Mattson, David J.; Reid, Matthew M. 1991. Conservation of the Yellowstone grizzly bear. *Conservation Biology*. 5: 364-372.
- Mattson, David J.; Reinhart, Daniel P. 1987. Grizzly bear, red squirrels, and whitebark pine: third year progress report. In: Knight, Richard R.; Blanchard, Bonnie M.; Mattson, David J. Yellowstone grizzly bear investigations: report of the Interagency Study Team, 1986. Bozeman, MT: U.S. Department of the Interior, National Park Service, Interagency Grizzly Bear Study Team: 36-45.
- Mattson, David J.; Reinhart, Daniel P. 1990. Whitebark pine on the Mount Washburn massiff, Yellowstone National Park. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 106-117.
- Mattson, David J.; Reinhart, Daniel P.; Blanchard, Bonnie M. 1993. Variation in production and bear use of whitebark pine seeds in the Yellowstone area. In: Proceedings—conference on plants and their environments; 1991 September; Mammoth, WY. Denver, CO: U.S. Department of the Interior, National Park Service, Regional Office. [In press].
- Mealey, Stephen Patrick. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973-1974. Bozeman, MT: Montana State University. 158 p. Thesis.
- Murie, O. J. 1944. Progress report on the Yellowstone bear study. Mammoth, WY: U.S. Department of the Interior, National Park Service, Yellowstone National Park. 13 p.
- Pfister, Robert D.; Kovalchik, Bernard L.; Arno, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Intermountain Forest and Range Experiment Station. 174 p.
- Poelker, Richard J.; Hartwell, Harry D. 1973. Black bear of Washington. *Biol. Bull.* 14. Olympia, WA: Washington State Game Department. 180 p.
- Pritchard, Geoffrey T.; Robbins, Charles T. 1990. Digestive and metabolic efficiencies of grizzly and black bears. *Canadian Journal of Zoology*. 68: 1645-1651.
- Raine, R. M.; Kansas, J. L. 1990. Black bear seasonal food habits and distribution by elevation in Banff National Park, Alberta. In: International Conference on Bear Research and Management: Proceedings: 8: 297-304.
- Romme, William H.; Turner, Monica G. 1991. Implications of global climate change for biogeographic patterns in the greater Yellowstone ecosystem. *Conservation Biology*. 5(3): 373-386.
- Reinhart, Daniel P.; Mattson, David J. 1990. Red squirrels in the whitebark zone. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 256-263.
- Reinhart, Daniel P.; Mattson, David J. 1992. Grizzly bear and black bear habitat use in the Cooke City, Montana, area 1990-1991. Bozeman, MT: U.S. Department of the Interior, National Park Service, Interagency Grizzly Bear Study Team. 30 p.
- Schallenger, A.; Jonkel, C. J. 1980. Rocky Mountain East Front grizzly studies, 1979. Annual Report. Border Grizzly Project Special Report 39. Missoula, MT: Border Grizzly Project. 207 p.
- Schemmel, R. 1976. Physiological considerations of lipid storage and utilization. *American Zoologist*. 16: 661-670.
- Servheen, Christopher. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. *Journal of Wildlife Management*. 47(4): 1026-1035.
- Servheen, Christopher; Knight, Richard; Mattson, David; Mealey, Steven; Strickland, Dale; Varley, John; Weaver, John. 1986. Report to the IGBC on the availability of foods for grizzly bears in the Yellowstone ecosystem. Missoula, MT: U.S. Fish and Wildlife Service, Office of the Grizzly Bear Recovery Coordinator. 21 p.
- Steele, Robert; Cooper, Stephen V.; Ondov, David M.; Roberts, David W.; Pfister, Robert D. 1983. Forest habitat types of eastern Idaho-western Wyoming. Gen. Tech. Rep. INT-144. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 122 p.
- Stirling, Ian; Derocher, Andrew E. 1990. Factors affecting the evolution and behavioral ecology of the modern

- bears. In: International Conference on Bear Research and Management: Proceedings: 8: 189-204.
- Taylor, R. A. 1964. Columbian ground squirrel and cambium found in grizzly bear stomachs taken in the fall. *Journal of Mammalogy*. 45(3): 476-477.
- Tisch, Edward L. 1961. Seasonal food habits of the black bear in the Whitefish Range of northwest Montana. Missoula, MT: University of Montana. 108 p. Thesis.
- Weaver, T.; Forcella, F. 1986. Cone production in *Pinus albicaulis* forests. In: Shearer, Raymond C., comp. Proceedings—conifer tree seed in the Inland Mountain West symposium.; 1985 August 5-6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 68-76.
- Weaver, T.; Forcella, F.; Dale, D. 1990. Stand development in whitebark pine woodlands. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 151-155.

ECOLOGICAL RELATIONSHIP BETWEEN CLARK'S NUTCRACKER AND FOUR WINGLESS-SEED *STROBUS* PINES OF WESTERN NORTH AMERICA

Diana F. Tomback

Abstract—The Clark's nutcracker (*Nucifraga columbiana*) is an important seed disperser for at least four western North American *Strobos* pines: whitebark (*Pinus albicaulis*), limber (*P. flexilis*), Colorado pinyon (*P. edulis*), and singleleaf pinyon (*P. monophylla*). Nutcrackers share the role of pinyon pine seed disperser with the pinyon jay (*Gymnorhinus cyanocephalus*) and may also contribute to seed dispersal of southwestern white pine (*P. strobiformis*). All five species of pines have large, wingless seeds. In whitebark pine and the pinyon pines, ripe seeds are retained in cones.

In this paper I briefly review the ecological relationship between Clark's nutcracker (*Nucifraga columbiana*) and four pine species of the subgenus *Strobos* that depend on the nutcracker for seed dispersal. A fifth *Strobos* pine, southwestern white (*Pinus strobiformis*) may also be dispersed by Clark's nutcracker (see Benkman and others 1984), but the requisite studies have not yet been done.

This review is not intended to be exhaustive but rather to sketch the basics of these interactions, which are similar to those between the Eurasian nutcracker (*N. caryocates*) and five European and Asian *Strobos* pines.

GEOGRAPHIC DISTRIBUTIONS

The Clark's nutcracker ranges throughout much of the montane regions of the Western United States (AOU 1983). The eastern limits are the Black Hills of South Dakota and, irregularly, the pine forests of southwestern South Dakota and northwestern Nebraska, and east of the Rocky Mountain front. To the south, the nutcracker ranges into northern Baja California, and to the north into Canada along the Coast Mountains and Rocky Mountains (fig. 1).

The geographic boundaries of all four *Strobos* pines known to be dispersed by Clark's nutcrackers fall within the range of the nutcracker (Critchfield and Little 1966) (fig. 1). Whitebark pine (*Pinus albicaulis*, Subsection *Cembrae*) is a subalpine-to-treeline species that occurs from the Sierra Nevada north through the coast ranges and Northern Rocky Mountains into Alberta and British

Columbia. Limber pine (*Pinus flexilis*, Subsection *Strobi*), which occupies a wide elevational range, is distributed from southern California across the Great Basin to the Rocky Mountains and north into Alberta and British Columbia. Both the singleleaf pinyon (*Pinus monophylla*) and Colorado pinyon pine (*Pinus edulis*), which are also dispersed by pinyon jays (*Gymnorhinus cyanocephalus*) (see, for example, Ligon 1978), are lower treeline species in the Subsection *Cembroides*. The singleleaf pinyon pine ranges from eastern and southern California south to northern Baja California and through the Great Basin to western and northern Utah and southern Idaho. The Colorado pinyon pine occurs in Utah, Colorado, Arizona, and New Mexico.



Legend:







- | | | |
|---|--|--|
| — Range of Clark's Nutcracker |  <i>P. edulis</i> |  <i>P. monophylla</i> |
|  <i>Pinus albicaulis</i> |  <i>P. flexilis</i> |  <i>P. strobiformis</i> |
|  <i>P. cembroides</i> | | |

Figure 1—Geographic ranges of *Strobos* pines with large, wingless seeds in the Western United States and Canada.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Diana F. Tomback is Associate Professor of Ecology, Department of Biology and Center for Environmental Sciences, University of Colorado at Denver, Denver, CO 80217-3364.

In addition, Parry pinyon (*Pinus quadrifolia*) and Mexican pinyon pine (*Pinus cembroides*), which are lower elevation species, may occasionally be dispersed by Clark's nutcracker where their ranges overlap with the bird, but this has not been documented. Similarly, where the range of southwestern white pine (*Pinus strobiformis*, Subsection *Strobi*), overlaps with the nutcracker in southern Colorado, New Mexico, and Arizona, its seeds may be nutcracker-dispersed (see, for example, Benkman and others 1984); the ranges of both Mexican pinyon pine and southwestern white pine continue south into Mexico.

CONE AND SEED TRAITS OF PINES

Large, wingless seeds characterize the four *Strobis* pines routinely dispersed by Clark's nutcracker and southwestern white pine (table 1). In fact, the mean seed weights of all the wingless-seed *Strobis* pines that may be dispersed by Clark's and Eurasian nutcrackers (*Nucifraga caryocatactes*) ($\bar{x} = 0.279$) are significantly greater than the mean seed weights of wind-dispersed *Pinus* pines ($\bar{x} = 0.094$) (Wilcoxon test, $H = 15.93$, $P = 0.00006$) and also significantly greater than the weights for the winged, wind-dispersed *Strobis* pines ($\bar{x} = 0.057$; $H = 9.31$, $P = 0.0023$, Tomback and Linhart 1990).

The cones of whitebark pine are indehiscent and thus do not open after seeds have ripened (see, for example, Lanner 1982). In the pinyon pines, the cones open, but ripe seeds are held in depressions on cone scales by means of small flanges (see, for example, Vander Wall and Balda 1977). Both seed winglessness and seed retention in cones increase the chances that nutcrackers rather than wind will disperse the seeds (Tomback and Linhart 1990). In contrast, the cones of limber and southwestern white pine open when the seeds are ripe; however, some limber pine seeds may remain lodged in open cones as long as several weeks after ripening (Tomback 1988; Torick 1993). Discussions concerning the evolution of cone and seed traits of bird-dispersed pines may be found in Lanner (1980), Tomback (1983), and Tomback and Linhart (1990).

The cones of whitebark pine (Tomback 1978), pinyon pine (Vander Wall and Balda 1977), and limber pine (Benkman and others 1984; Tomback and Kramer 1980) ripen asynchronously within and among trees in late summer, providing a continuous seed supply for several weeks or more and allowing nutcrackers to disperse more of the seed crop. In contrast, the cones of southwestern white pine ripen synchronously both within and among trees,

Table 1—Mean seed weights of western *Strobis* pines dispersed by Clark's nutcracker. Data from table 3 in Tomback and Linhart 1990

Pine species	Mean weight
	Grams
Singleleaf pinyon (<i>Pinus monophylla</i>)	0.4086
Colorado pinyon (<i>P. edulis</i>)	.2387
Whitebark (<i>P. albicaulis</i>)	.1745
Southwestern white (<i>P. strobiformis</i>)	.1680
Limber (<i>P. flexilis</i>)	.0926

Table 2—Maximum sublingual pouch capacities of Clark's nutcracker for four *Strobis* pines. Scientific names of pines as in table 1

Pine species	Maximum number of seeds	Reference
Whitebark	100-150	Tomback 1982; Tomback and Knowles 1989
Limber	120	Vander Wall 1988
Colorado pinyon	95	Vander Wall and Balda 1977
Singleleaf pinyon	38	Vander Wall 1988

which may result in the dispersal of a smaller percentage of the seed crop (Benkman and others 1984).

SEED HARVESTING AND CACHING BY NUTCRACKERS

The morphology and behavior of the Clark's nutcracker are similar to those of the Eurasian nutcracker. The Clark's nutcracker has a long, sharp bill that is used to stab into and loosen closed cone scales or to remove seeds from open cones (see Tomback 1978 for details of seed harvesting behavior). Nutcrackers transport pine seeds in the sublingual pouch, a sac that is formed by the floor of the mouth and opens under the tongue (Bock and others 1973). Maximum seed capacities of the pouch vary with the pine species (table 2). In addition, nutcrackers have a remarkable spatial memory that enables them to relocate their seed stores accurately for more than 9 months after caching them (Balda and Kamil 1992; Kamil and Balda 1985; Tomback 1980; Vander Wall 1982).

Clark's nutcrackers may begin eating unripe seeds from the cones of whitebark (Hutchins and Lanner 1982; Tomback 1978) and limber pine (Tomback and Taylor 1987) as early as mid to late July in some years. A bird exposes the unripe seeds by stabbing its bill between cone scales and tearing off scale pieces. Usually only bits of unripe seeds can be extracted at this time. Nutcracker-damaged cones increase in frequency throughout summer. In limber pine they are particularly noticeable: where nutcrackers removed seeds, red-brown patches of frayed cone material contrast against the green, undamaged cone scales.

When seeds are ripe and extracted from cones at a relatively rapid rate (Hutchins and Lanner 1982; Tomback 1978; Vander Wall 1988), nutcrackers begin to cache them. Nutcrackers have stored whitebark pine seeds as early as August 15 in the Rocky Mountains (Hutchins and Lanner 1982) and August 25 in the Sierra Nevada (Tomback 1978). For limber pine and both pinyon pines, dates of first seed storage are similar in different montane areas: late August to early September (Tomback and Kramer 1980; Tomback and Taylor 1987; Vander Wall 1988; Vander Wall and Balda 1977).

Nutcrackers cache seeds at distances from a few meters to 22 km from parent trees. Vander Wall and Balda (1977)

determined that some nutcrackers carried Colorado pinyon seeds 7.5 to 22 km to caching areas, and Tomback (1978) determined that nutcrackers traveled as far as 8 to 12 km with whitebark pine seeds. More typical distances are shorter and up to a few kilometers (Hutchins and Lanner 1982; Tomback 1978; Vander Wall 1988).

In addition to traveling moderate to long distances, nutcrackers may fly to higher or lower elevations to store seeds. For example, nutcrackers in the eastern Sierra Nevada cache whitebark pine seeds not only at subalpine elevations (2,700 to 3,000 m) but also at 2,100 m to 2,400 m in the mixed Jeffrey pine (*Pinus jeffreyi*) and singleleaf pinyon pine forest (Tomback 1978). Similarly, nutcrackers carrying Colorado pinyon seeds in northern Arizona may fly up 300 m elevation to caching areas (Vander Wall and Balda 1977). In the Colorado Front Range, nutcrackers were observed to carry bristlecone pine (*Pinus aristata*) seeds from the subalpine forest up several hundred meters toward tundra for caching (Baud 1993).

Clark's nutcrackers cache seeds both in communal storage areas, often characterized by steep, south-facing slopes (Tomback 1978; Vander Wall and Balda 1977), and in terrain not far from parent trees (Tomback 1978). The Eurasian nutcracker, in contrast, caches many of its seeds in a year-round territory (see, for example Mattes 1982). Seeds are usually buried 1 to 3 cm under gravelly soil, mineral soil, or duff (Hutchins and Lanner 1982; Tomback 1978), although a small number may be hidden in hollows, under bark, in cracks, and in holes in trees and in logs (Tomback 1978; Torick 1993). Each cache typically consists of one to 15 seeds, although larger caches may occasionally be made; mean cache sizes are three or four seeds (Tomback and Linhart 1990, table 5 and references therein; Torick 1993).

The specific kinds of sites selected by nutcrackers for burying seed caches include the following: near the base of trees; around tree roots, fallen trees, and branches; around rocks and boulders; on rocky, exposed ledges; within sparse to heavy plant cover and moss; at the edge of grassy meadows; and within stands of krummholz pine forms (Hutchins and Lanner 1982; Tomback 1978, 1986; Tomback and Kramer 1980; Tomback and Taylor 1987; Vander Wall and Balda 1977). In addition, nutcrackers bury seeds at and above treeline (Baud 1993) and in burned forest terrain (Tomback 1986; Tomback and Knowles 1989).

Estimates of how many seeds are stored by a single Clark's nutcracker vary geographically and with the pine species. For whitebark pine, Tomback (1982) estimated that about 35,000 seeds per individual were cached after a good cone crop in the eastern Sierra Nevada, but the nutcracker then cached the seeds of other pine species, such as Jeffrey pine or singleleaf pinyon pine, or even limber pine (Tomback and Kramer 1980). Hutchins and Lanner (1982) estimated that a single nutcracker cached as many as 98,000 whitebark pine seeds in western Wyoming. According to Vander Wall and Balda (1977), one nutcracker in northern Arizona stored between 22,000 and 33,000 Colorado pinyon pine seeds following a good cone crop. For northern Utah, Vander Wall (1988) calculated that one nutcracker stored a maximum of 16,000

limber pine seeds and a maximum of about 18,000 singleleaf pinyon seeds.

In all cases the stored seeds provided several times the amount of energy required by one nutcracker during the period that the seed stores were used (see, for example, Tomback 1982; Vander Wall and Balda 1977). The excess stored seeds probably provided a margin for loss of caches to rodents, feeding caches to young, and some "forgetting" of seed cache location (see, for example, Balda and Kamil 1992; Tomback 1982).

PHENOLOGY OF USE AND SPECIES PREFERENCE

In much of the montane Western United States and southern Canada, more than one nutcracker-dispersed *Strobos* pine occurs in the same geographic area (fig. 1). For example, in the Northern Rocky Mountains whitebark pine typically occurs at subalpine elevations and limber pine at the lower forest boundary, although in some locations the two species may co-occur in the subalpine zone. In years when both species produce cones, nutcrackers preferentially harvest and store whitebark pine seeds before moving into limber pine forests (Tomback 1992). Similarly, in the eastern Sierra Nevada, whitebark pine, limber pine, and singleleaf pinyon occur in the same region; whitebark pine seeds are harvested and stored before limber pine and singleleaf pinyon pine seeds (Tomback 1978; Tomback and Kramer 1980). In both regions, nutcrackers may prefer to take whitebark pine seeds first, because the cones ripen earlier than do limber pine or pinyon pine cones.

In the Raft River Mountains of northern Utah, stands of limber pine and singleleaf pinyon pine occur only a few kilometers apart. When cone crops of both species were available, most nutcrackers harvested and stored limber pine seeds before using pinyon pine seeds (Vander Wall 1988). Limber pine cones ripened before pinyon pine cones in this area. When limber pine and Colorado pinyon pine both produced cone crops in northern Arizona, Vander Wall and Balda (1977) observed nutcrackers harvesting and caching seeds from the closed, green cones of both species at the same time in late summer. These examples suggest that species preference is probably based on cone ripening sequence.

Clark's nutcrackers are also known to harvest and store the seeds of several wind-dispersed pine species of both the subgenus *Strobos* and *Pinus*. Stomach contents analysis of Clark's nutcrackers collected in western Montana indicated that the birds ate, if not cached, ponderosa pine (*Pinus ponderosa*) seeds and Douglas-fir (*Pseudotsuga menziesii*) seeds in addition to whitebark pine seeds (Giuntoli and Mewaldt 1978). Nutcrackers regularly harvest and cache seeds of Jeffrey pine in the eastern Sierra Nevada (Tomback 1978). Lanner (1988) noted nutcracker-damaged cones of Great Basin bristlecone pine (*Pinus longaeva*) in the Wasatch Range and in the Great Basin. In the Front Range of the Colorado Rockies, Torick (1993) observed nutcrackers harvest and cache ponderosa pine seeds, and Baud (1993) observed nutcrackers harvest and transport bristlecone pine seeds

to caching areas. Baud (1993) recently obtained experimental evidence that both bristlecone pine and ponderosa pine seedlings may be routinely established from nutcracker caches. This has been indirectly confirmed by Torick (1993) who has shown that the tree cluster growth form, which is found in several nutcracker-dispersed pines and arises from multiseed nutcracker caches (Tomback and Schuster, these proceedings, and references therein), also occurs in ponderosa and bristlecone pine.

ACKNOWLEDGMENTS

Support to the author for attending the SSPE Workshop was provided by the College of Liberal Arts and Sciences, University of Colorado at Denver. I thank Lisa Torick and Karen Baud for comments on an earlier draft of this paper.

REFERENCES

- American Ornithologists' Union. 1983. Check-list of North American birds. 6th ed. Lawrence, KS: American Ornithologists' Union. 877 p.
- Balda, R. P.; Kamil, A. C. 1992. Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. *Animal Behavior*. 44: 761-769.
- Baud, K. S. 1993. Germination rates and losses to rodents of artificial nutcracker caches of three species of *Pinus* placed in three elevational zones in the Colorado Front Range. Data on file, Department of Biology, University of Colorado at Denver.
- Benkman, C. W.; Balda, R. P.; Smith, C. C. 1984. Adaptations for seed dispersal and the compromises due to seed predation in limber pine. *Ecology*. 65: 632-642.
- Bock, W. J.; Balda, R. P.; Vander Wall, S. B. 1973. Morphology of the sublingual pouch and tongue musculature in Clark's nutcracker. *Auk*. 90: 491-519.
- Critchfield, W. F.; Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. Misc. Publ. 991. Washington, DC: U.S. Department of Agriculture, Forest Service. 97 p.
- Giuntoli, M.; Mewaldt, L. R. 1978. Stomach contents of Clark's nutcracker collected in western Montana. *Auk*. 95: 595-598.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Kamil, A. C.; Balda, R. P. 1985. Cache recovery and spatial memory in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*. 11: 95-111.
- Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. In: Dancik, B. P.; Higginbotham, K. O., eds. Sixth North American forest biology workshop: proceedings. Edmonton, AB: University of Alberta: 15-48.
- Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. *Canadian Journal of Forest Research*. 12: 391-402.
- Lanner, R. M. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevations. *Arctic and Alpine Research*. 20: 358-362.
- Ligon, J. D. 1978. Reproductive interdependence of piñon jays and piñon pines. *Ecological Monographs*. 48: 111-126.
- Mattes, H. 1982. Die Lebengemeinschaft von Tannenhäher und Arve. Birmensdorf, Switzerland: Swiss Federal Institute of Forestry Research. 74 p.
- Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. *Living Bird*. 16: 123-161.
- Tomback, D. F. 1980. How nutcrackers find their seed stores. *Condor*. 82: 10-19.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology*. 51: 451-467.
- Tomback, D. F. 1983. Nutcrackers and pines: coevolution or coadaptation? In: Nitecki, M. H., ed. *Coevolution*. Chicago: University of Chicago Press: 179-223.
- Tomback, D. F. 1986. Post-fire regeneration of krummholz whitebark pine: a consequence of nutcracker seed caching. *Madroño*. 33: 100-110.
- Tomback, D. F. 1988. Nutcracker-pine mutualisms: multi-trunk trees and seed size. In: Ouellet, H., ed. *Acta XIX Congressus Internationalis Ornithologici*, Vol. I; 1986 June 22-29. Ottawa, ON: University of Ottawa Press: 518-527.
- Tomback, D. F. 1992. Observations in the Wind River Range. Unpublished data on file, Department of Biology, University of Colorado at Denver.
- Tomback, D. F.; Knowles, J. W. 1989. Post-fire whitebark pine seed dispersal by Clark's nutcracker in Yellowstone National Park. Unpublished data on file, Department of Biology, University of Colorado at Denver.
- Tomback, D. F.; Kramer, K. A. 1980. Limber pine seed harvest by Clark's nutcracker in the Sierra Nevada: timing and foraging behavior. *Condor*. 82: 467-468.
- Tomback, D. F.; Linhart, Y. B. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology*. 4: 185-219.
- Tomback, D. F.; Taylor, C. L. 1987. Tourist impact on Clark's nutcracker foraging activities in Rocky Mountain National Park. In: Singer, F., ed. *Wildlife management and habitats*. Washington, DC: National Park Service and George Wright Society: 158-172.
- Torick, L. L. 1993. Field and laboratory evidence for regeneration of wind-dispersed pines from animal-dispersed caches. Data on file, Department of Biology, University of Colorado at Denver.
- Vander Wall, S. B. 1982. An experimental analysis of cache recovery in Clark's nutcracker. *Animal Behavior*. 30: 84-94.
- Vander Wall, S. B. 1988. Foraging of Clark's nutcrackers on rapidly changing pine seed resources. *Condor*. 90: 621-631.
- Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of Clark's nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs*. 47: 89-111.

Forest Structure and Dynamics



International Workshop
St. Moritz 1992

STRUCTURE OF SWISS STONE PINE STANDS IN NORTHEASTERN ITALY

Giovanna De Mas
Elena Piutti

Abstract—This contribution suggests a structural typology for Swiss stone pine (*Pinus cembra*) stands in the eastern range of the Italian Alps. Study of the structure in these stands makes it possible to understand their dynamics and to evaluate environmental and scenic aspects of the present expansion of high-elevation forests. This paper describes eight structural types that show different rhythms in the forest establishment process.

The structure of Swiss stone pine (*Pinus cembra* L.) stands has been studied by several authors, although with different methodological approaches (see, for examples, Contini and Lavarello 1981, 1982; Del Favero and others 1985; Kuoch 1972; Mayer and Ott 1991; Piussi and Schneider 1985; Rachoy 1976; Schiechl and Stern 1975, 1979, 1983, 1984; Stern and Helm 1979). These studies are of particular interest. They allow one to make an improved assessment of management and environmental implications resulting from reforestation of high-elevation abandoned pastures. These have become a typical feature of many alpine areas as a consequence of changed economic structures.

In fact, since the structure analysis of a tree stand provides a detailed description of the spatial and temporal tree distribution pattern, these early approaches are necessary to understand the complex mechanisms that control natural regeneration and intra- and interspecific competition. Moreover, they enable us to quantify rhythms of different tree species establishment and to define the complex stand-stability degree. The objective of this investigation, which is part of the INTEGRALP project financially supported by EEC, is to detect early structure types of stone pine stands on the southern slope of the eastern Alps. Knowledge of these stands is comparatively scanty.

FIELD SURVEYS

Field work was carried out in a large part of the autonomous Province of Bolzano and in the Province of Belluno. In particular, the study was conducted in stone pine

coenoses in the following valleys of Bolzano Province: Venosta, Passiria, Sarentino, Funes, Luson, Gardena, and Badia and in Cortina basin in Belluno Province. This scenic area exhibits a remarkable climatic and geologic variability.

Climate becomes increasingly continental while moving from east to west (Del Favero and others 1985; Fliri 1975). Temperatures are moderate in the east and annual precipitation exceeds 1,000 mm, with rainfall maxima in spring and autumn. In the west, climate gradually becomes colder in winter, and summers are dry and hot. Annual precipitation is less than 1,000 mm and the rainfall regime is continental. Geological substrata change from limestone in the east to silicate bedrock in the west.

In the eastern part, stone pine is found at the eastern periphery of its natural range. It forms pure or mixed forests associated with larch (*Larix decidua* Mill.) and/or spruce (*Picea abies* Karst.). It is occasionally mixed with Scots pine (*Pinus sylvestris* L.) or with silver fir (*Abies alba* Mill.). The vegetational aspects of these associations were described by Filipello and others (1976; 1980-81).

Based on the results of field surveys and on data available from forest management plans, it was possible to make a preliminary early subdivision of the stone pine stands examined into comparatively homogeneous structure categories. These categories range from open stands of remarkably large-size trees, sometimes accompanied by recent young trees, to more or less closed forests.

First, a rough classification was conceived. Then, some forest stands were subjectively identified by size and variability of the category itself. These stands were considered to approximately represent the specific structure conditions. In each of these stands, a rectangular 400-m² sample plot was marked. In this plot, the following parameters were recorded for each tree exceeding a diameter of 7.5 cm at ground level: breast height diameter, height, age at tree base, distance of tree center from the two plot vertices. Then, spatial tree distribution (vertical and horizontal) was drawn with early processing and the following stand parameters were computed per hectare: number of trees, basal area, volume (determined using the double entry volume tables of the National Forest Inventory, I.S.A.F.A., 1984), average diameter, and average height.

In total, 39 sample plots were surveyed. Their main characteristics are summarized in table 1. Subjective sampling and the selection of a comparatively low number of small sample plots was inevitable because of limited funding and in view of the objective of analyzing at least the most important stands among those observed.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Giovanna De Mas is a Researcher and Elena Piutti is making her research doctorate stage, Land and Agro-Forest Environment Department, University of Padova, 35100 Padova, Italy.

Table 1—Main parameters for the sample plots investigated. Locality abbreviations: Ga = Gardena; Ba = Badia; Fu = Funes; Lu = Lusón; Ve = Venosta; Se = Senales; Pa = Passiria; Sa = Sarentino; and Co = Cortina

Plot number	Locality	Elevation	Aspect	No. of trees/ha	Basal area/ha	Composition				Volume/ha	Average diameter	Average height	Maximum height	Age of oldest tree
						Stone pine	Larch	Spruce	Others					
		Meters			m ²	-----	-----	-----	-----	m ³	cm	-----	-----	Years
1	Ga	1,550	S	550	19.6	10		59	31	152.5	21.3	14.0	24.0	178
2	Ga	1,750	S	575	26.2	26		57	17	211.0	24.1	19.0	20.5	184
3	Ga	1,900	SE	625	32.4	70		30		250.1	25.7	18.1	21.5	216
4	Ga	2,100	E	575	22.7	99				113.7	22.4	10.2	11.5	95
5	Ba	1,600	N	250	18.6	8		84	8	188.4	30.8	22.5	28.5	181
6	Ba	1,750	N	575	24.0	30	45	25		239.8	23.1	18.2	27.0	171
7	Ba	1,940	N	425	19.1	29	59	12		138.9	23.9	11.8	23.0	178
8	Ba	2,020	N	425	18.8	25	75			126.1	23.7	12.7	16.5	247
9	Fu	1,850	N	575	37.2	70	4	26		263.0	28.7	15.0	22.0	233
10	Fu	1,980	E	425	21.4	99				129.5	25.3	10.1	14.5	170
11	Fu	1,750	N	425	67.4	59	29	12		720.8	44.9	20.5	33.0	225
12	Fu	2,135	SO	450	31.1	99				218.9	29.6	13.3	18.0	235
13	Lu	1,710	SE	475	33.4	37		63		221.0	29.9	15.0	18.0	175
14	Lu	1,620	SE	650	20.1	27	4	69		151.9	19.8	14.9	26.5	170
15	Lu	2,050	SO	550	18.7	99				90.3	20.8	8.9	13.0	107
16	Lu	2,200	E	625	14.9	99				54.9	17.4	7.1	11.5	133
17	Ve	1,760	ENE	1,050	32.9	43	5	52		260.2	20.0	15.7	21.5	180
18	Ve	1,850	NE	750	24.8	90	10			151.4	20.5	11.4	18.0	155
19	Ve	2,100	SW	875	28.8	94	6			181.9	20.5	10.5	21.0	190
20	Ve	2,260	WSW	140	28.8	99				211.1	51.2	13.4	21.0	280
21	Ve	1,760	NW	600	23.1	92	8			148.4	22.1	13.7	16.2	170
22	Ve	1,840	NE	600	38.4	71	21	4	4	289.7	28.5	14.3	22.8	210
23	Ve	1,950	NW	875	27.1	94	6			167.8	19.9	12.3	14.8	135
24	Ve	1,970	SW	425	39.2	77	17	6		318.6	34.3	16.4	24.8	170
25	Se	2,100	N	625	35.4	88	12			314.7	26.8	12.9	23.0	403
26	Se	1,950	NE	225	13.0	87	13			87.1	27.1	12.5	18.0	247
27	Se	2,050	NE	400	55.0	87	13			494.1	41.8	21.0	23.5	360
28	Se	2,000	NE	425	19.5	65	35			126.0	24.2	11.6	19.5	163
29	Pa	1,675	NE	600	21.6	99				129.1	21.4	10.1	15.0	103
30	Pa	1,850	NE	575	13.0	86	4		10	75.2	17.0	11.3	16.5	95
31	Sa	1,857	NNW	525	10.1	62		38		88.3	15.7	18.0	19.5	145
32	Sa	1,525	NNW	675	42.6	96	4			385.9	28.3	18.7	23.0	205
33	Sa	1,600	NNW	425	24.1	88	12			181.7	26.9	13.3	25.0	150
34	Sa	1,750	N	375	41.0	43	7	50		443.9	37.3	22.5	27.0	210
35	Sa	1,950	NW	575	54.3	64	18	18		510.5	34.7	18.9	25.5	220
36	Sa	1,880	NNE	450	45.5	28		72		454.2	35.9	22.8	26.0	210
37	Sa	1,680	NNE	875	55.4	63	6	31		491.5	28.4	19.5	23.5	270
38	Co	2,180	E	1,100	24.6	38	62			121.9	16.9	9.6	16.0	131
39	Co	1,850	E	400	35.7	30	20	50		230.4	33.7	18.2	21.0	207

METHODS

As mentioned earlier, the structural analysis of a forest stand enables us to describe its appearance and to understand its dynamics—the patterns and the mechanisms that have controlled its development until now. The present state results from the interaction between natural components and human disturbances.

The structure of a forest coenosis can be illustrated by means of its characteristics or by “chronological” elements. The former can be sampled and observed more easily. They allow a static view of stand conditions that can be described in detail. For this purpose, the following elements are considered in general: composition (numeric and volumetric), percentage of tree number in diameter classes (usually 5-cm range) and in height classes (of different width), related to total sum of trees, numeric indices of spatial distribution, and some dendrometric parameters.

In this investigation, the elements given were taken into consideration for each sample plot. However, only the following ones were used in the assessment of structural types: numeric composition, diameter classes, relative height classes related to three layers, and ratio of variance with mean of number of trees found in the four subplots, each 100 m² wide, into which the sample plot had been divided.

The chronological structure of a stand provides a picture of the stand dynamics and of species establishment. Thus the chronological aspect is essential for structure analysis, although it is often neglected because of surveying difficulties. Its identification is made by subdividing the number of trees, distinguished by tree species, into chronological classes with an unstandardized range (in the case considered in this work, a 20 years' lapse rate was fixed).

To develop an early structural typology for the stands investigated, we tried to aggregate sample plots into homogeneous groups. Distance measures were computed using Minkowski's algorithm (Franceschetti and Provasi 1978) taking the physical and chronological factors into consideration, after having standardized data and converting them into percentages of the totals.

Because of the unsatisfactory results obtained in this early processing, another method was tried. Three sets of sample plots, different in composition, were selected. The first set (17 sample plots) includes those where stone pine represents over 80 percent of the species composition; the second (14 plots) includes those where stone pine is present by less than 80 percent; spruce prevails, or is the second species by importance. The third set (eight plots) comprises those where larch prevails or is the second species after stone pine (which is in any case present by less than 80 percent). Then, the distance measure computation was repeated in each of these three sets, considering as factors only the ones concerning the physical structure.

Before discussing the results, it is necessary to state that no case-by-case assessment could be made of the modifications that cutting or grazing caused on the structure of the single sample plots, because they were hardly

noticeable on small-size areas. It is only possible to believe that both activities were carried on in the areas investigated and the dynamism that led to the present structure was affected by severe cuts made in the past and by the progressive abandonment of grazing practices.

RESULTS

Five stand structure types (fig. 1) are distinguished in the first set of sample areas where stone pine is present by over 80 percent. Three types, however, are based on one observation only.

The first type (fig. 2, structural type 1.1), includes six sample plots. Diameter distribution decreases as diameter increases, with trees that reach the 55-cm class. As to vertical distribution, a remarkable concentration of heights is found in the intermediate layer, although a fair share occurs in the upper third.

In the second type (fig. 3, structural type 1.2, eight sample plots), the regeneration process occurred gradually as tree age ranges from 20 to 220 years. Most of them are 101 to 120 years old, while a few exceed 140 years. Diameter distribution is different; it is unimodal with a maximum in the 20-cm class and with a high concentration in the 15- to 30-cm classes. Vertical distribution shows most heights in the upper third.

In the third type (fig. 4, structural type 1.3), the stand has a reduced number of trees per hectare (140 trees/ha), and trees are missing at the youngest age. The last new generation occurred 60 to 140 years ago. The height distribution of trees appears well balanced in the layers, even if a slight trend to one-storied formation can be noticed.

Contrary to that, in the fourth type (fig. 5, structural type 1.4), regeneration appears to be more recent because the new generation comprises trees 40 to 80 years old. Tree heights concentrate in the lower third just as do the diameters, which are mainly found within the 10- to 20-cm classes.

The last type (fig. 6, structural type 1.5) represents the structural conditions of a comparatively rare pure even-aged stone pine stand where all mature individuals are over 220 years old while younger trees are missing. Trees (400/ha) have diameters varying from 30 to 60 cm and heights concentrated in the third upper layer.

Three types are distinguished in the second set. They concern sample plots where stone pine is less than 80 percent and spruce is either prevailing or the second species.

In the first type (fig. 7, structural type 2.1), including five sample plots, diameters range from 10 to 50 cm and exhibit a bimodal-type pattern with a main maximum in the 30-cm class and a secondary maximum in the 20-cm class. Trees are concentrated in the 20- to 35-cm classes. The high number of trees in the 10-cm class (youngest individuals) should be emphasized; this reflects well-established regeneration. As to vertical distribution, a trend to one-storied stand formation is evident since over 60 percent of the trees are included in the upper third.

From the chronological point of view, a slight uneven-age structure is apparent. It is characterized by a wide range of tree ages varying from 20 to over 220 years.

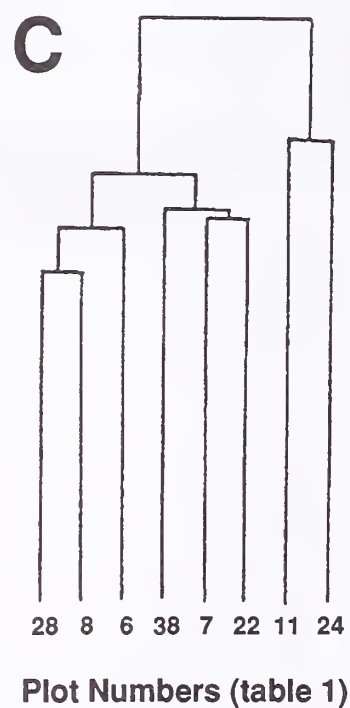
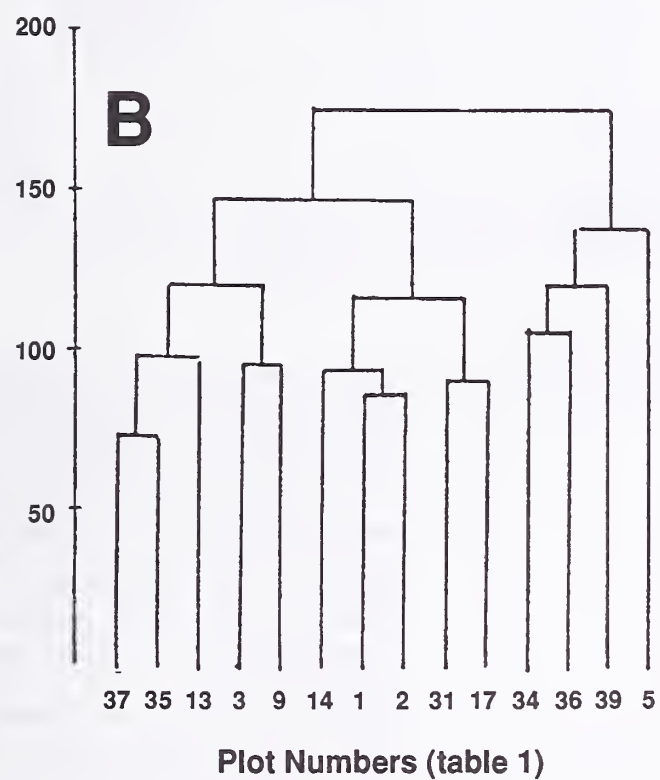
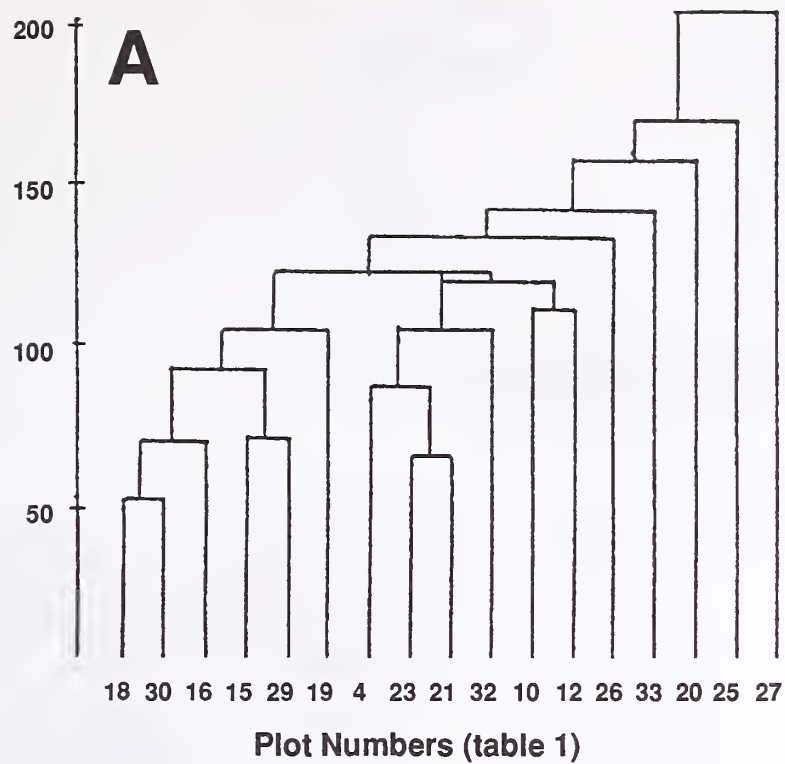


Figure 1—Dendrograms obtained from the measurements of distance among the elements of physical structure. A, set of stone pine plots; B, set of stone pine and spruce plots; C, set of stone pine and larch plots.

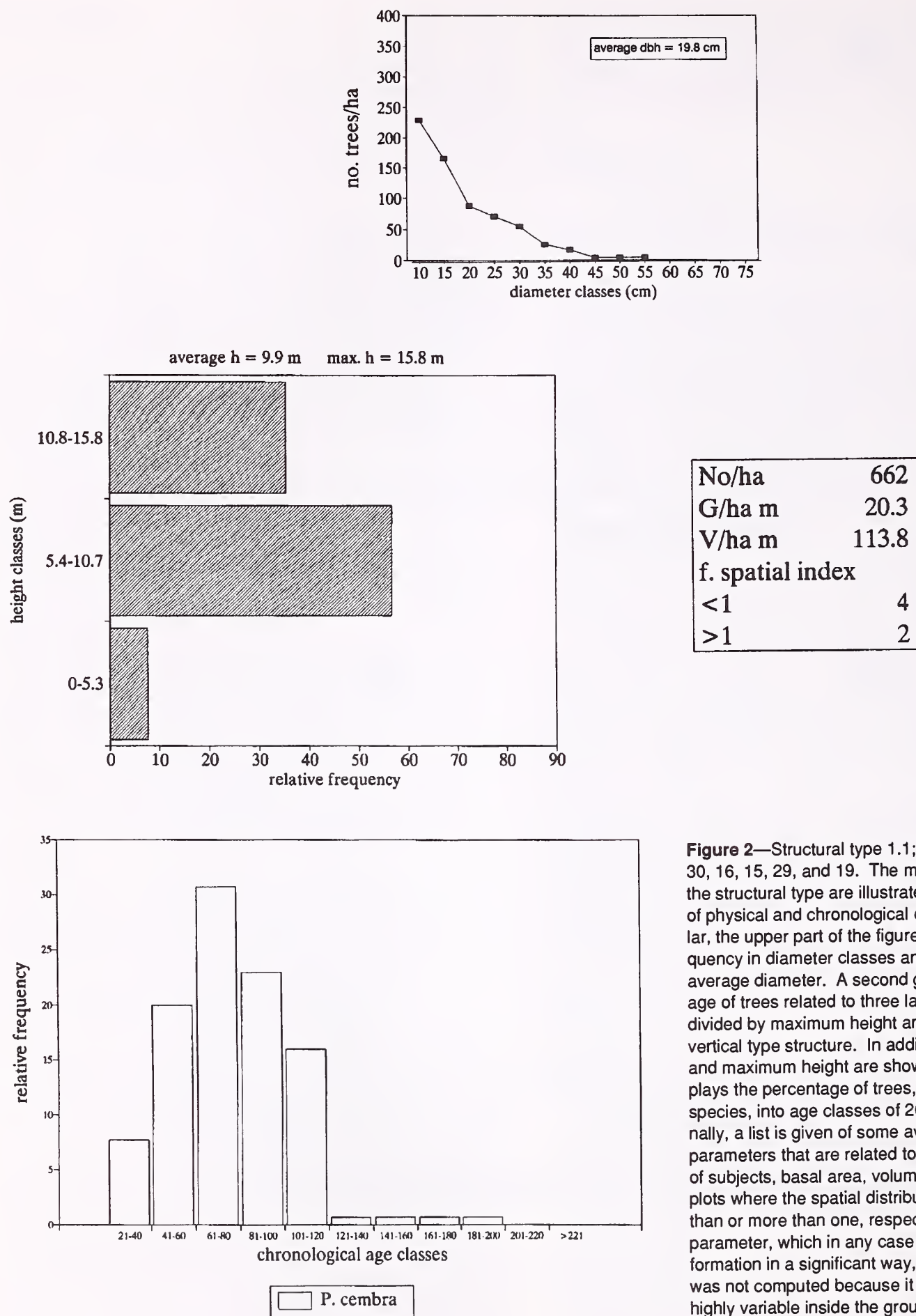
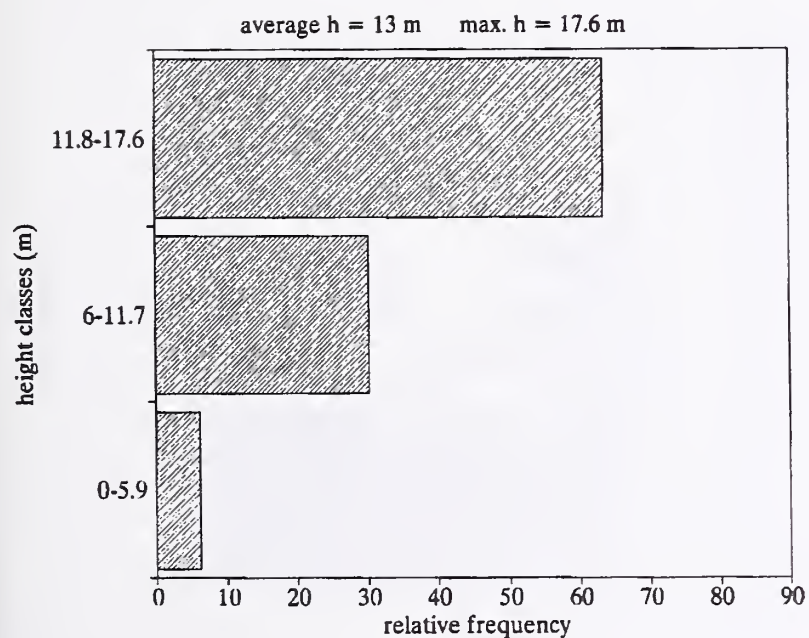
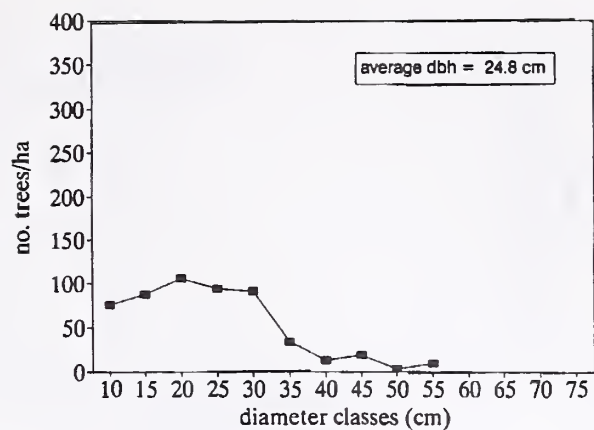


Figure 2—Structural type 1.1; including plots 18, 30, 16, 15, 29, and 19. The main characteristics of the structural type are illustrated by average values of physical and chronological elements. In particular, the upper part of the figure shows tree frequency in diameter classes and the value of the average diameter. A second graph shows percentage of trees related to three layers. These are subdivided by maximum height and represent the vertical type structure. In addition, average height and maximum height are shown. A third graph displays the percentage of trees, distinguished by tree species, into age classes of 20 years' width. Finally, a list is given of some average dendrometric parameters that are related to the hectare (number of subjects, basal area, volume) and the number of plots where the spatial distribution index is less than or more than one, respectively. For this last parameter, which in any case never affected type formation in a significant way, the average value was not computed because it often proved to be highly variable inside the group.



No/ha	531
G/ha m	25.6
V/ha m	179.1
f.spatial index	
<1	2
>1	6

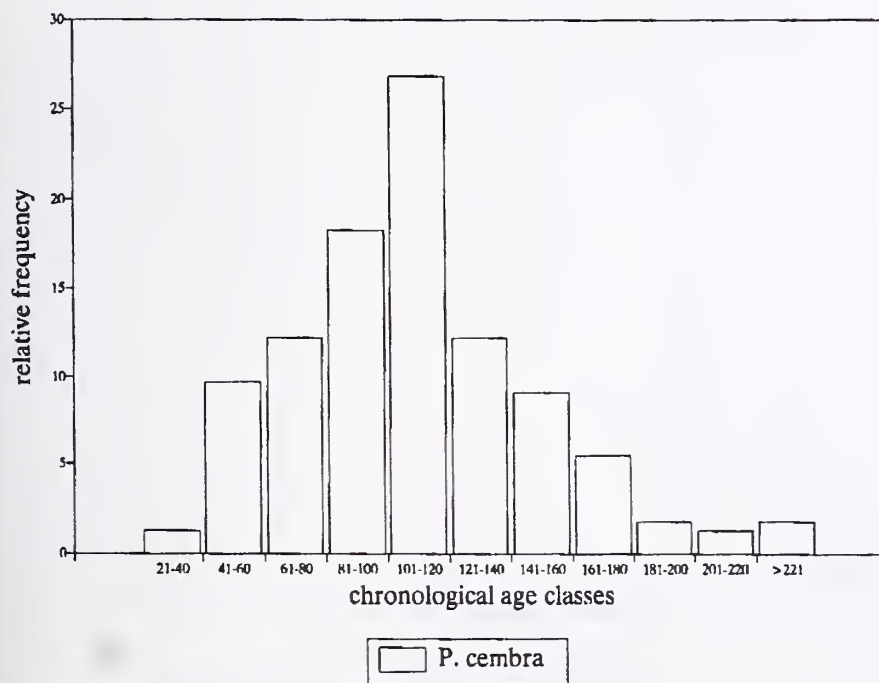
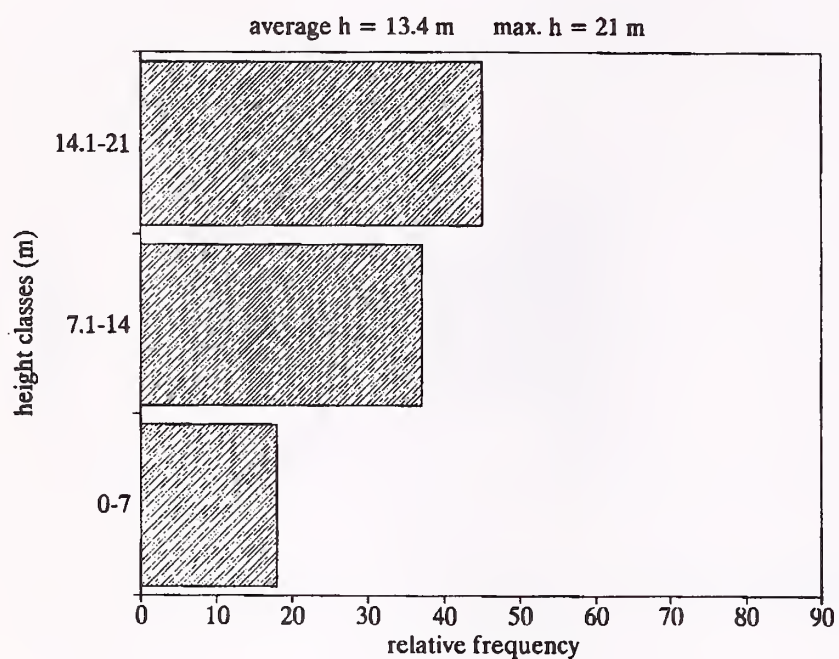
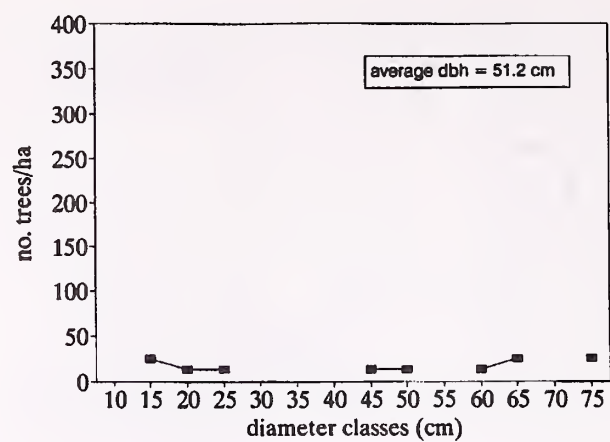


Figure 3—Structural type 1.2; including plots 4, 23, 21, 32, 10, 12, 26, and 33.



No/ha	140
G/ha m	28.8
V/ha m	211.1
f. spatial index	
<1	1
>1	0

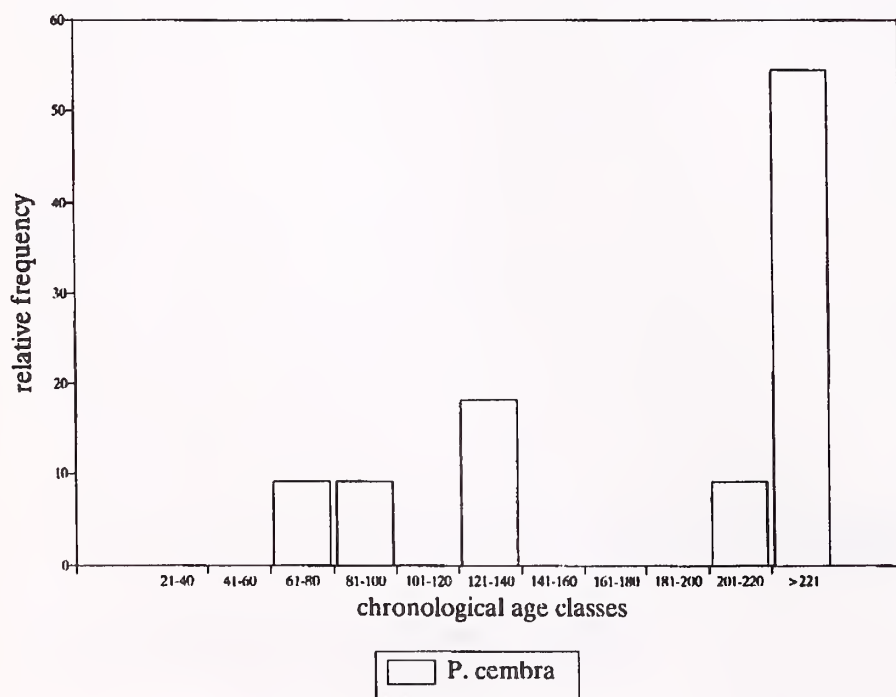
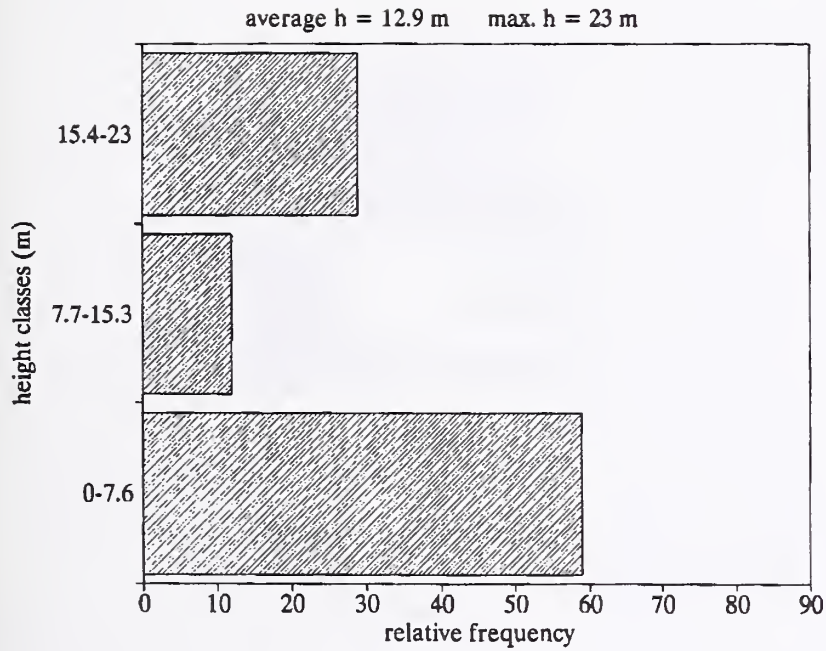
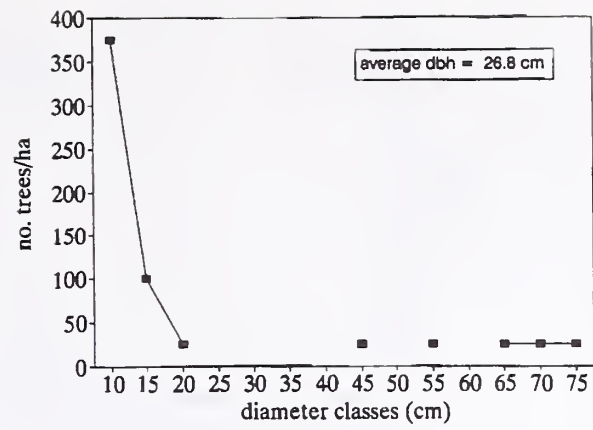


Figure 4—Structural type 1.3; including plot 20.



No/ha	625
G/ha m	35.4
V/ha m	314.7
f. spatial index	
<1	0
>1	1

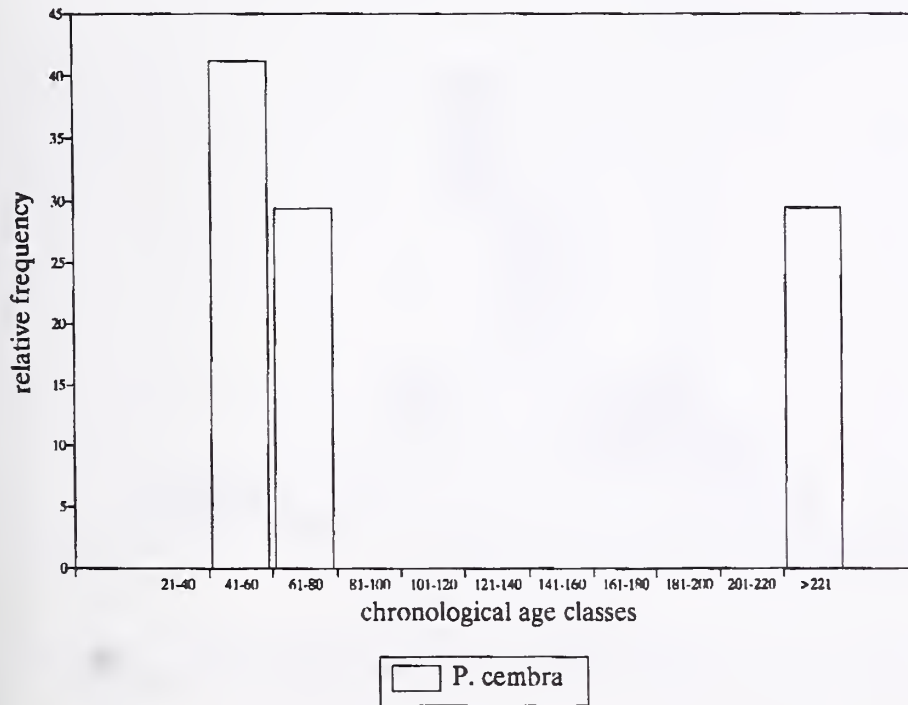
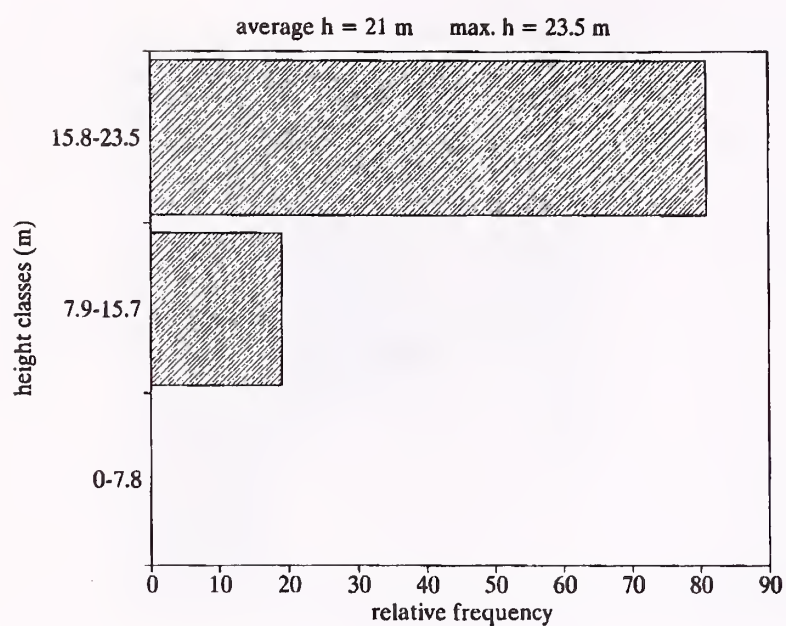
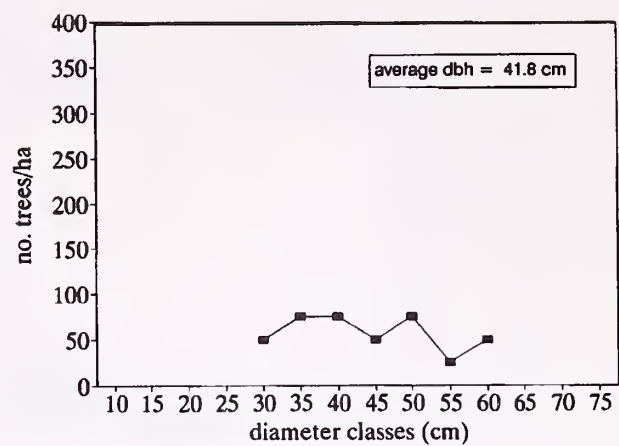


Figure 5—Structural type 1.4; including plot 25.



No/ha	400
G/ha m	55
V/ha m	494.1
f. spatial index	
<1	1
>1	0

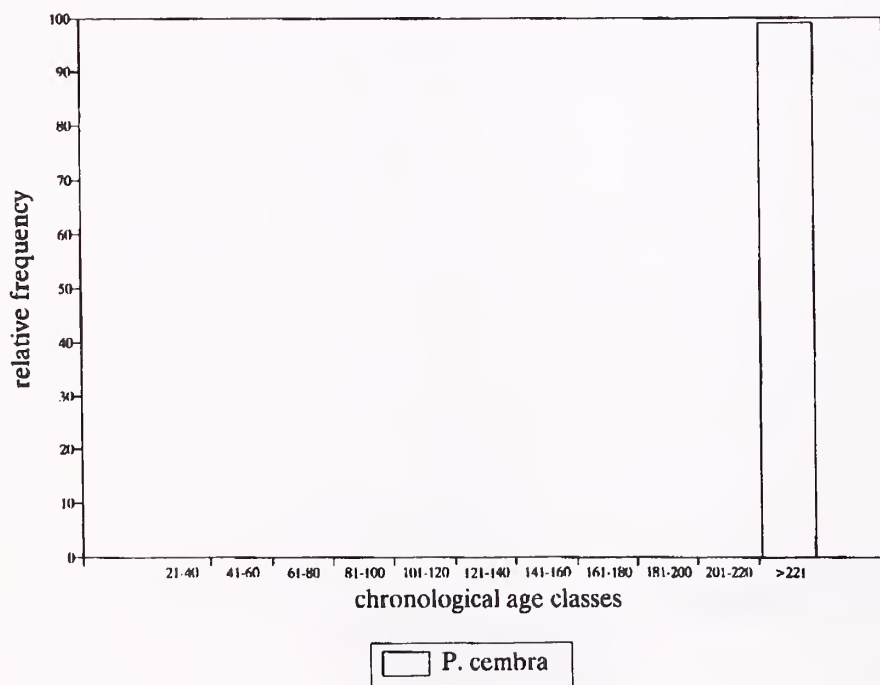
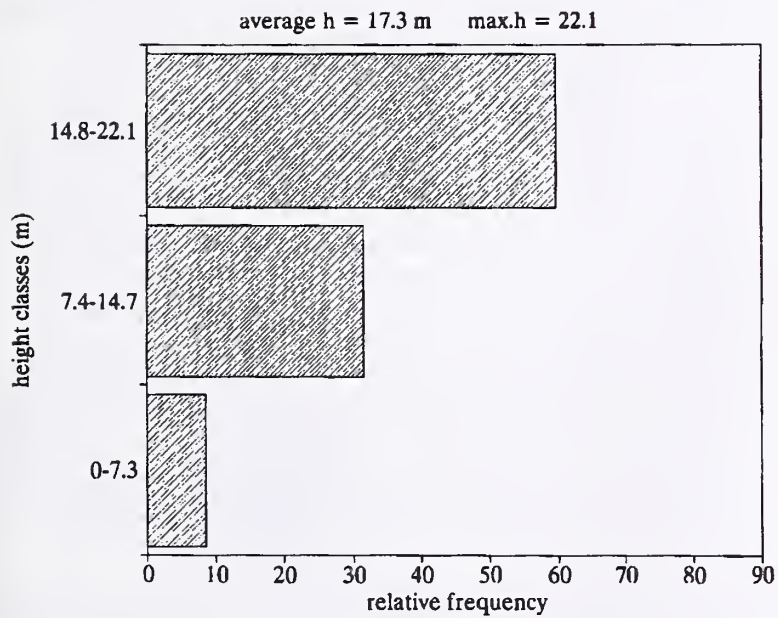
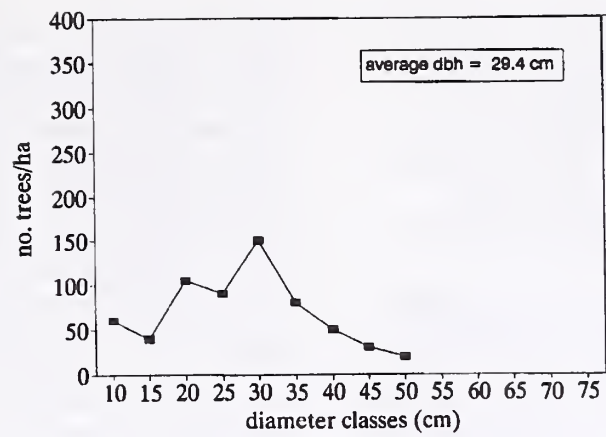


Figure 6—Structural type 1.5; including plot 27.



No/ha	625
G/ha m	42.5
V/ha m	347.2
f. spatial index	
<1	2
>1	3

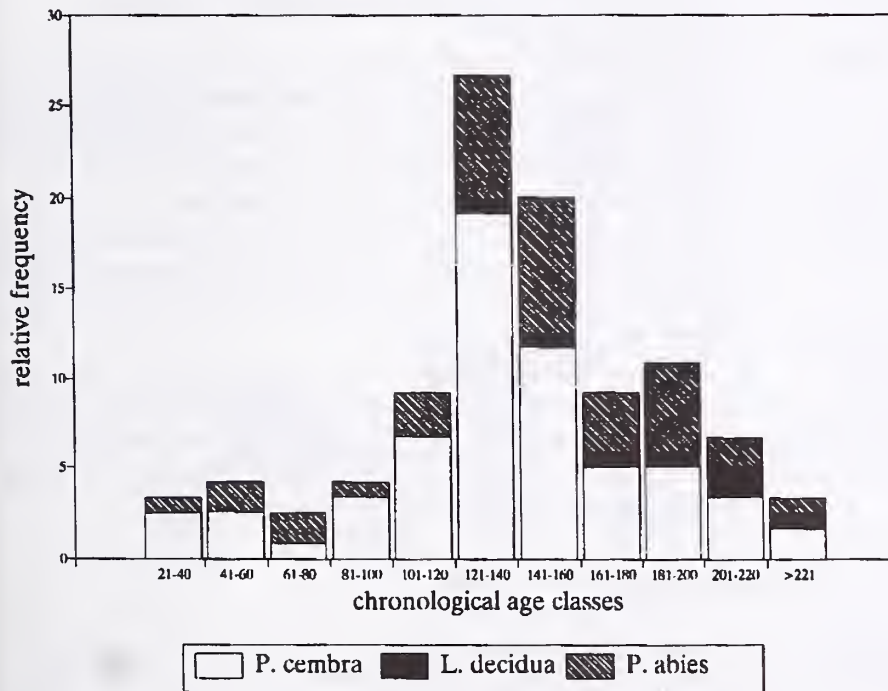


Figure 7—Structural type 2.1; including plots 37, 35, 13, 3, and 9.

There is, however, a large quantity of trees in the 121- to 160-year classes, with a maximum in the class of 121 to 140 years. Moreover, larch is conspicuous only in the advanced age classes (from 120 years and older, with a maximum in the 201- to 220-year class). In this type, the average number of trees per hectare amounts to 625, basal area per hectare is 42.5 m², while average volume per hectare turns out to be 347.2 m³.

The second type (fig. 8, structural type 2.2), including four sample plots, shows a wider diameter range (from 10 to 70 cm). A trend can be clearly noticed for unimodal distribution with a maximum in the 40-cm class. A fair variability can be observed also in the upright tree distribution. In fact, individuals with heights in the upper layer prevail; nevertheless individuals in the lower third are well represented.

A slight uneven-age condition can also be noticed in this second type (ages range from 20 to 220 years), but age distribution is more regular with 141- to 160-year classes prevailing. The average values are 369 trees per hectare, basal area is 35.2 m², and volume is 329.2 m³.

The last type of the second group (fig. 9, structural type 2.3) includes five sample plots and, in contrast with those so far examined, it has a decreasing diameter distribution with a high number of small- or middle-size trees that are not strictly found in the younger chronological classes. Height distribution is more uniform. There is a larger one-storied formation, because nearly 90 percent of the trees form the two upper layers. Moreover, differences in age are slightly less conspicuous (40 to 200 years). Most trees are in the 80 to 140 classes. The number of trees per hectare (670) is comparatively high, while the many small-size trees lower the value for basal area (21.8 m²) and for volume (172.8 m³) per hectare. The decreased proportion of larch is emphasized and confirms what already has been stated. Larch less than 80 years is not represented in this case; instead other species (Scots pine and silver fir) join in the formation.

In the third set, including areas where stone pine is represented by less than 80 percent and larch is either predominant or the second species, it should be noted that aggregations obtained through distance measures do not seem to be satisfactory because of extreme stand differences. Consequently, it was impossible to single out groups representing average conditions. It may be that only a subsequent closer investigation with an increased number of observations will enable us to define a structural typology for these coenoses. Larch is found either in the oldest chronological classes or in the young classes, where structures are more open.

DISCUSSION

For the first two sets of stand structure, homogeneous structural types can be interpreted from the chronological point of view. The third set was different.

In the first type, physical elements show a structure characterized by an intermediate layer that is sufficiently differentiated by competition and is mixed with remarkably large-size trees from a previous stand. Taking into consideration age distribution, few trees older than 120

years can be observed. Most of the stand, however, consists of trees with ages ranging from 20 to 120 years, but with a peak in the 60- to 80-year class. Thus it can be supposed that in this case regeneration has occurred within a comparatively short time, and is now decreasing gradually. The stands have a good number of trees per hectare (662). Conversely, the other dendrometric parameters (all of them rather low) suggest that biospace will be saturated chiefly by a growth increase of individuals already present rather than by additional trees.

Conversely, in the second type the physical and chronological aspects and the dendrometric parameters, which are higher than in the previous type (531 trees/ha, 25.6 m²/ha basal area, 179.1 m³ mass-volume-stock/ha) suggest that biospace filling processes are more advanced and that the formation is structurally more stable.

As already stated, the three types that complete the structural typology of the first set are each represented by only one observation. They illustrate structural conditions that are not very frequent but clearly distinct from those examined so far. In particular, the third and fourth type distinctly display some possible early stages of the regeneration process, since two clearly different generations coexist at the same time. A high proportion of trees over 220 years of age can be observed in both types, while the remaining individuals fall within younger classes. The structure of the third type can be easily explained considering that the plot is located at the treeline (2,260 m). This is an environment where the regeneration process occurs only occasionally or it may be entirely missing for a long time. The latter seems to have happened in this case.

In the fourth type, the large number of trees per hectare (625) suggests that the future structure in this stand should be similar to the first two types described.

The last type, as already pointed out, represents a rather rare situation.

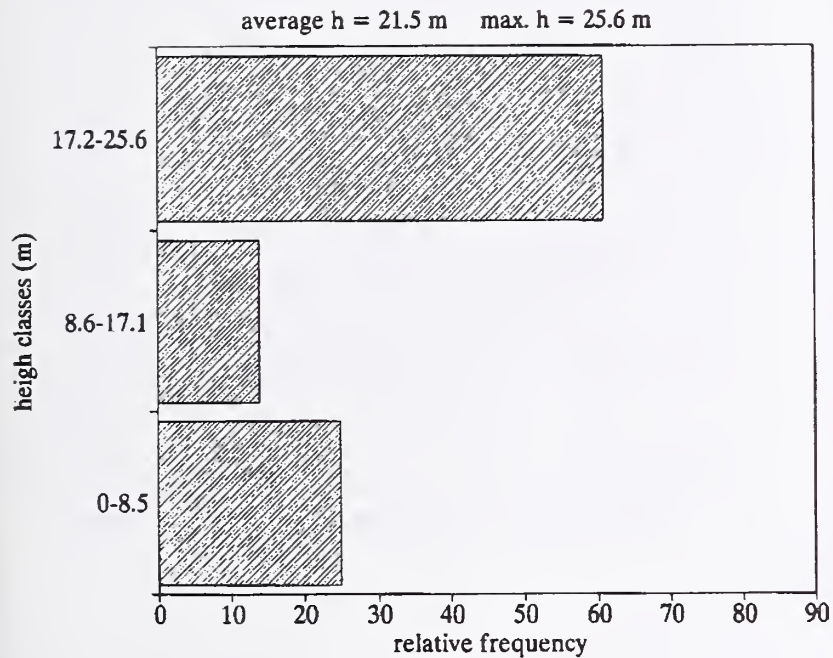
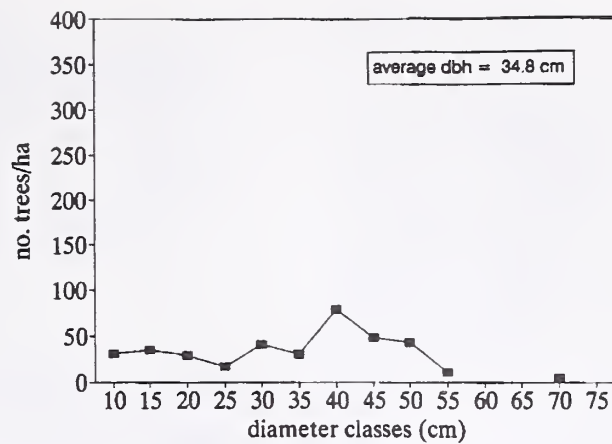
In the first type of the second set, the chronological analysis suggests that the stand originated from a grazed forest. Spruce, as well as stone pine, is represented in all classes, which means that there was a continuous invasion of these two species into the formation.

The second type is characterized by formations that are open grown, permitting new spruce and stone pine to continuously invade the stand. However, larch regeneration ended about 80 years ago.

In the last type, regeneration occurred rapidly and a sufficiently closed stand established in a short time. After that, regeneration slowed down, but competition among individuals increased. That caused the diameter differentiation mentioned earlier.

CONCLUSIONS

From the methodological point of view, the use of distance measures has made it possible to point out a structural typology in stands where stone pine, or spruce with stone pine, are clearly predominant. These results were obtained using physical structure elements as discriminating factors. Other results—more difficult to interpret—were obtained that take into consideration both physical and chronological elements.



No/ha	369
G/ha m	35.2
V/ha m	329.2
f. spatial index	
<1	1
>1	3

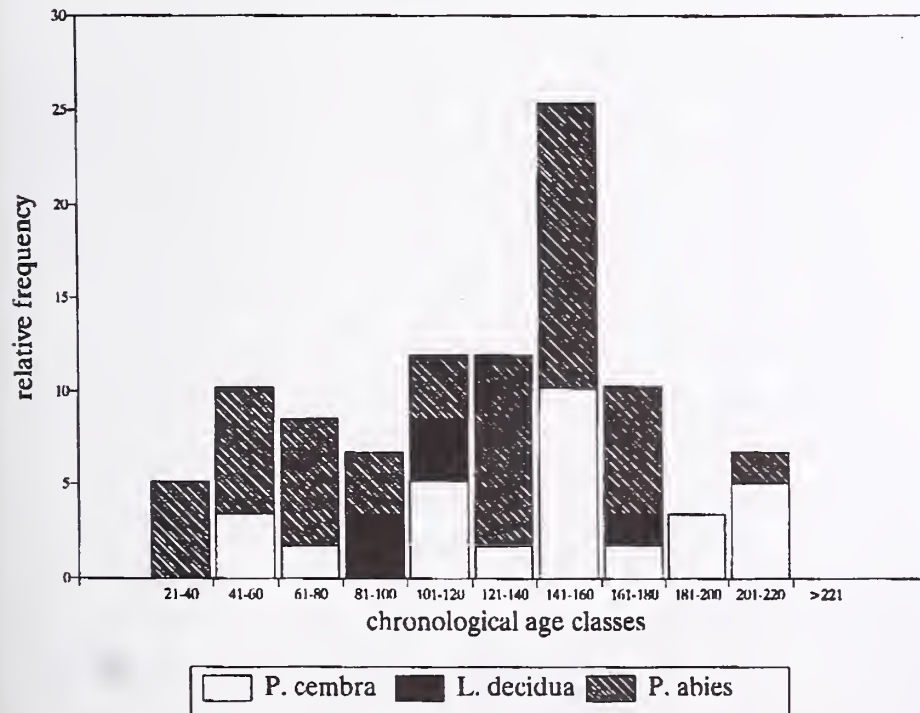
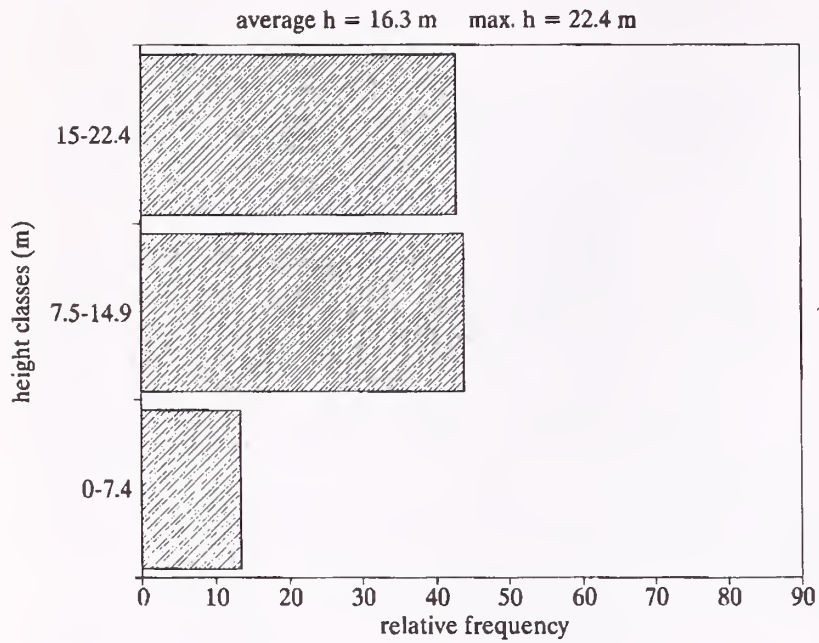
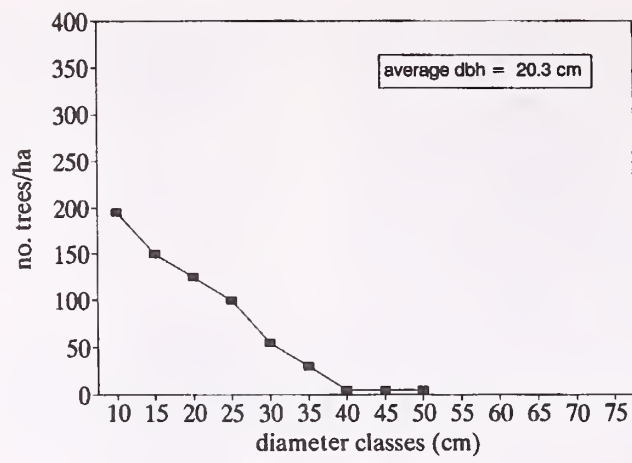


Figure 8—Structural type 2.2; including plots 5, 34, 36, and 39.



No/ha	670
G/ha m	21.8
V/ha m	172.8
f. spatial index	
<1	2
>1	3

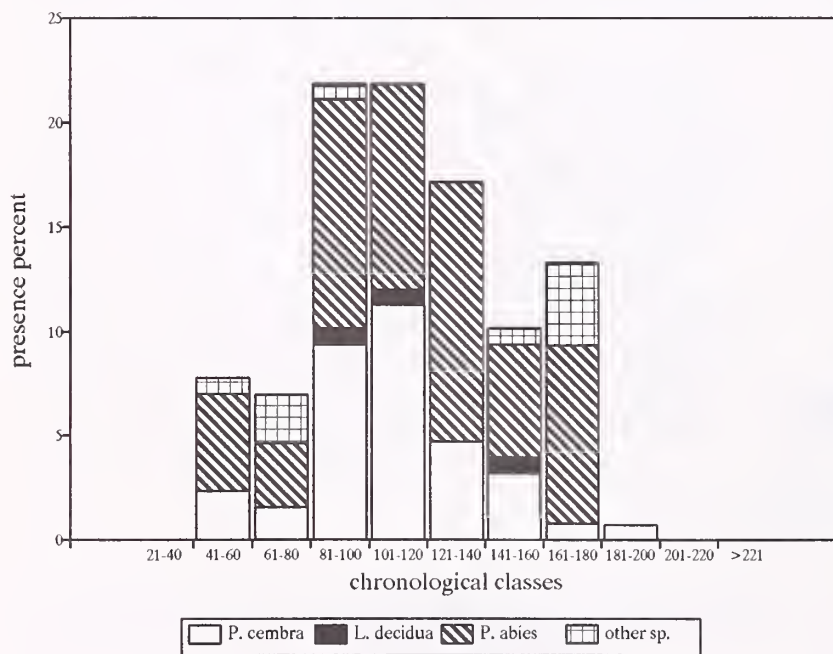


Figure 9—Structural type 2.3; including plots 14, 1, 2, 31, and 17.

The structural typology defined, though rather variable, shows that the regeneration process started about one century ago, and it sometimes developed in a gradual and continuous way and at other times more quickly and massively. Generally, it is possible to observe good structures in physical and chronological elements. These will probably provide these stands with sufficient stability.

REFERENCES

- Contini, L.; Lavarelo, Y. 1981. Le pin cembro: répartition, écologie et croissance. CNRF, Nancy. 254 p.
- Contini, L.; Lavarelo, Y. 1982. Le pin cembro: végétation, écologie, Sylviculture et production. INRA, Paris. 197 p.
- Del Favero, R.; De Mas, G.; Lasen, C.; Paiero, P. 1985. Il pino cembro nel Veneto. Assessorato Agric. e For., Dip. per le foreste e l'economia montana, Venezia. 85 p.
- Filipello, S.; Sartori, F.; Vittadini, M. 1976. Le associazioni del cembro sul versante meridionale dell'arco alpino. Atti Istituto Botanica Università di Pavia. 11: 21-104.
- Filipello, S.; Sartori, F.; Vittadini, M. 1980-1981. Le associazioni di cembro nel versante meridionale dell'arco alpino. 2: La vegetazione: aspetti forestali. Atti Istituto Botanica Università di Pavia. 14: 1-48.
- Fliri, F. 1975. Das Klima der Alpen im Raume von Tirol. Universitaets-Verlag Wagner, Innsbruck-Munchen. 454 p.
- Franceschetti, G.; Provati, C. 1978. La cluster analysis quale strumento di zonizzazione nella pianificazione. In: Metodologia per la formazione dei piani zonali agricoli nella Regione Veneto. Istituto Estimo Rurale e Contabilità, Università di Padova: 32-90.
- I. S. A. F. A. 1984. Inventario forestale nazionale. Tavole di cubatura a doppia entrata. Trento. 111 p.
- Kuoch, R. 1972. Zur Struktur und Behandlung von Subalpinen Fichtenwaeldern. Schw. Zeit. fur Forst. 123(2): 77-89.
- Mayer, H.; Ott, E. 1991. Gebirgswaldbau Schutzwaldpflege. 2 Auflage, Gustav Fischer Verlag Stuttgart-New York.
- Piussi, P.; Schneider, A. 1985. I limiti superiori del bosco e degli alberi in Val di Vizze (prov. di Bolzano). Annali Acc. It. Sc. Forestali: 121-150.
- Rachoy, W. 1976. Waldbauliche Strukturuntersuchungen in subalpinen Zirbenwaeldern. Invited Papers, Congress Group 1, XVI. IUFRO-World-Congress, Oslo 1976: 183-202.
- Schiechtl, H. M.; Stern, R. 1975. Die Zirbe (*Pinus cembra* L.) in den Ostalpen. I Teil, Angew. Pflanzensoz. 22: 1-83.
- Schiechtl, H. M.; Stern, R. 1979. Die Zirbe (*Pinus cembra* L.) in den Ostalpen. II Teil, Angew. Pflanzensoz. 24: 1-79.
- Schiechtl, H. M.; Stern, R. 1983. Die Zirbe (*Pinus cembra* L.) in den Ostalpen. III Teil, Angew. Pflanzensoz. 27: 1-110.
- Schiechtl, H. M.; Stern, R. 1984. Die Zirbe (*Pinus cembra* L.) in den Ostalpen. IV Teil, Angew. Pflanzensoz. 28: 1-99.
- Stern, R.; Helm, G. 1979. Alter und Struktur von Zirbenwäldern. Allgem. Forstr. 90: 194-198.

ROLE OF *PINUS PUMILA* IN PRIMARY SUCCESSION ON THE LAVA FLOWS OF VOLCANOES OF KAMCHATKA

S. Yu. Grishin

Abstract—The succession of the subalpine vegetation was studied on the lava flows of the Central Kamchatka. The rate of succession depends on type of lava and the formation of friable substratum on lava surface following ash falls and other causes. Stone pine (*Pinus pumila*) is not a pioneer on the original lava surface. Rather, its main role is determined during the first half of succession (0 to 1,000 years). During this period it forms closed communities and soil cover, favoring the establishment of other dominant species in the subalpine zone. During the second half of succession (1,000 to 2,000 years) *P. pumila* decreases to the cover level typical for climax vegetation. Thus the role of *P. pumila* is unique; it restores vegetation cover on juvenile substrate.

Many thousand square kilometers of Kamchatka's territory are covered by layers of lava flows. Most of the territory has subalpine vegetation. Under these conditions the subalpine stone pine (*Pinus pumila*) (nomenclature of all species follows Czerepanov 1981) is the most important species forming plant cover on juvenile substrate. This species usually forms dense communities in the subalpine belt

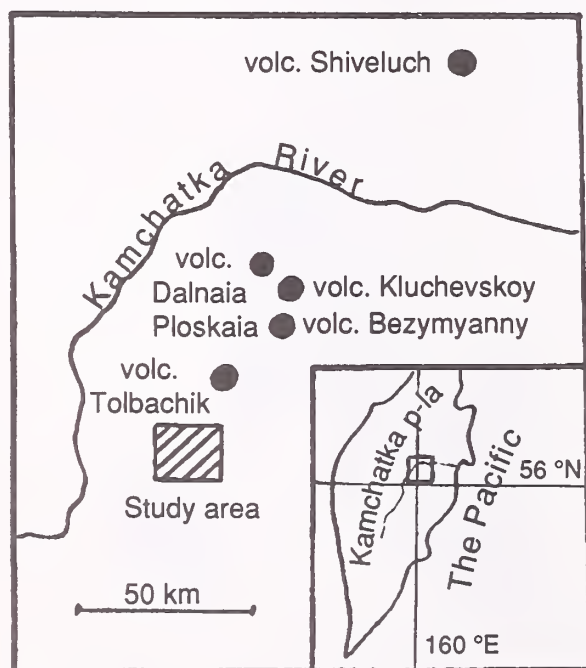


Figure 1—Location of study area.



Figure 2—Tolbachik volcano (altitude 3,682 m).

in northeastern Asia. At Kamchatka, p-la *P. pumila* may be found from the seashore to the mountain slopes up to 1,400 m above sea level. It covers 42 percent of the forest-covered territory.

This study was conducted in the Central Kamchatka, near Tolbachik volcano (figs. 1 and 2). During the Holocene, lava flows formed a lava plateau with an area of 875 km². The lava flows of Kluchevskoy volcano were also investigated. The age of the flows was determined by the tephra-chronology method, based on radiocarbon dating (Braitseva and others 1981). With this method we could distinguish the stages of succession and estimate their duration (Grishin 1992).

The climatic conditions of the Tolbachik area reveal a continental pattern, similar to the climate of Middle Siberia. The mountain vegetation is composed by forests of spruce (*Picea ajanensis*) and larch (*Larix kamtschatica*) up to an altitude of 500 m, while birch (*Betula ermanii*) occurs up to 900 m. The subalpine zone is situated at the interval of 800 to 1,100 m. It has a complex structure: forest islands of birch, open woodlands of larch, vast covers of stone pine and alder (*Duschekia kamtschatica*) krummholz, patches of subalpine meadows and alpine-type communities. The alpine belt extends to 2,000 m altitude, and the snowline lies near 2,500 m (Grishin 1988a,b).

In the summer of 1975 in the central part of the plateau there was a major eruption. As a result of this, lava flows with an area of about 9 km² were effused and tephra (volcanic ash, sand, and scoria) was dispersed on 470 km². This

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

S. Yu. Grishin is Research Scientist at the Institute of Biology and Pedology of Far East Branch of Russian Academy of Sciences, Vladivostok-22 690022, Russia.



Figure 3—Volcanic plateau of the Tolbachik area: lava flows covered by tephra and remnants of larch trees and *Pinus pumila* krummholz.

layer has a depth of more than 0.1 m (fig. 3). The vegetation was completely destroyed on 400 km² (Fedotov 1984).

ROLE IN SUCCESSION

The investigation of the lava flows (10 to 50 years old) showed that *P. pumila* is not a pioneer species actively establishing on the juvenile substrata of pahoehoe (ropy lava), aa (scoria lava), and tephra. Herbaceous plants (*Chamerion angustifolium*, *Poa malacantha*, *Leymus ajanensis*, and others), mosses (*Polytrichum* spp.), and lichens (*Stereocaulon vesuvianum*) establish most actively initially. Woody plants such as poplar (*Populus suaveolens*), some willows, and very occasionally larch and stone birch establish less readily—all the plants settle on the friable substratum (tephra, products of weathering of lava, and others). Seedlings of *P. pumila* were rather rare, appearing a few years



Figure 4—Seedling of *Pinus pumila* on aa lava.

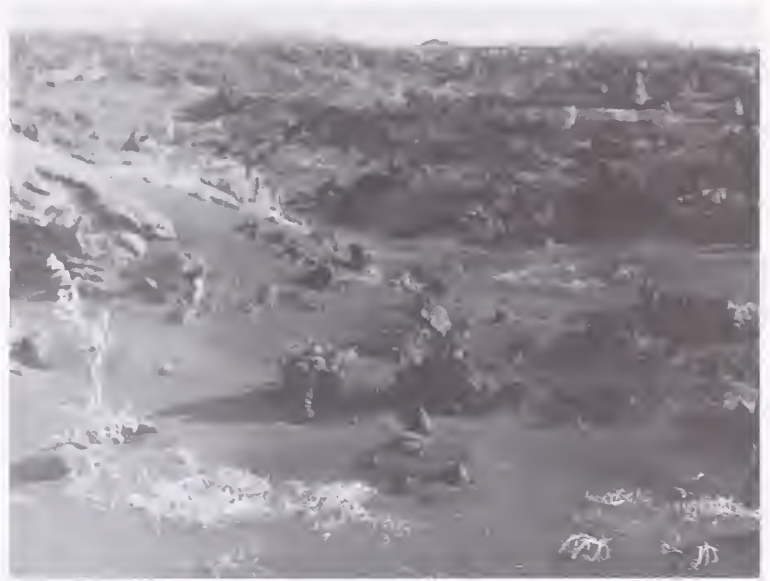


Figure 5—Lava flow about 500 years old covered by tephra to a depth of about 40 cm.

after the eruption (fig. 4). The difficulties in its distribution are because its seeds are dispersed by animals and seed sources 5 to 10 km away. Five hundred years later, scattered herbaceous and shrubby vegetation is formed on lava surface with single (about 10 trees/ha), extremely stunted (3 to 5 m height) larch trees. Low thickets of *P. pumila* (0.3 to 0.5 m height) dominate the vegetation, covering about 30 percent of the surface (fig. 5). *Pinus pumila* fills all potential habitats with friable substratum and forces out the herbaceous pioneer species. Under the tephra deposit on blocks and plates of lava, a thin layer (1 to 3 cm) of primitive soil develops. *Pinus pumila* is rooted in crevices between blocks on concentrated friable substratum enriched with organic matter (fig. 6).

On the 1,000-year-old lava flows, more closed vegetation can be observed. *Pinus pumila* is the dominant species and covers 60 to 90 percent of the surface (fig. 7). Its height



Figure 6—The remnants of stunted larch and branches of *Pinus pumila* between blocks of lava.



Figure 7—The flow of aa lava about 1,000 years old.

reaches 1 to 1.5 m. The characteristic feature of this stage of succession is the appearance of dominants of new communities. The most important plant in the new communities is alder krummholz. It settles on the substratum prepared by *P. pumila*, which eventually disappears from the slopes of the lava ridge and occurs only in the flat bottoms between ridges (fig. 8). Together with stone pine, slowly growing small larch trees (a few dozen trees/ha) are found. The abundant leaf fall of the alder and of the undergrowth plants (*Calamagrostis langsdorffii*, and others) considerably accelerates the rate of succession and prepares the substratum for stone birch—a very important dominant tree in the subalpine forest. The depth of the soil on different lava flows is 5 to 15 cm.

During the next 500 years (1,000 to 1,500 years old) the rate of succession increases noticeably, leading to differentiation of vegetation in the subalpine zone. On the 1,500-year-old

lava flows, typical subalpine communities can be distinguished. In addition to the dominant *P. pumila* thickets, the single clumps of alder, and the open woodlands of larch, communities of stone birch, covers of alder, subalpine meadows, and fragments of alpine heath appear. At this point, the coverage of *P. pumila* decreases, occupying its own typical habitats such as rock crests, concave hollows with frozen soils, and wind-exposed sites. The thickness of the soil profile increases to 20 cm, and the leveling of volcano-genic microrelief begins to occur. Both coenotical and vertical differentiation of vegetation takes place. During the earlier stage of succession, *P. pumila* dominated at altitudes from 200 to 1,000 m, but to this stage the forest belt below 800 m is formed, composed of larch and stone birch.

On the 2,000- and 2,500-year-old lava flows the vegetation was destroyed completely by the ash fall of 1975 (fig. 9). Its remnants give evidence that vegetation cover had been approaching the climax stage. It had mature communities with well-developed trees and krummholz, the size and cover of which were related to their altitudinal position. For example, at one of the flows at the altitude of 700 m a well-developed birch-larch subalpine forest with some spruce was located. The birch trees had a height of more than 10 m and a diameter at breast height of 25 to 40 cm. The larch trees were about 20 m and 30 to 40 cm, respectively. The alder krummholz under the forest layer had a height of 2.5 to 3 m, and *P. pumila* heights were 1.5 to 2 m.

These examples show that under such conditions, beginning at the age of 1,500 years, the vegetation tends to approach the climatic climax similar to the neighboring localities. Many criteria prove it.

The peculiarities of succession are determined mainly by the pattern of lava cover and the accumulation of friable substratum on the lava surface. On pahoehoe lava, establishment of plants on the smooth monolith surface is an extremely slow process. After the first 1,000 years of such lithosere, the lava is commonly covered only by crustaceous lichens. Higher plants settle on friable substratum in cracks and cavities, and that is in fact the beginning of psammose (fig. 10). Even if these plants are rooted in lava, they

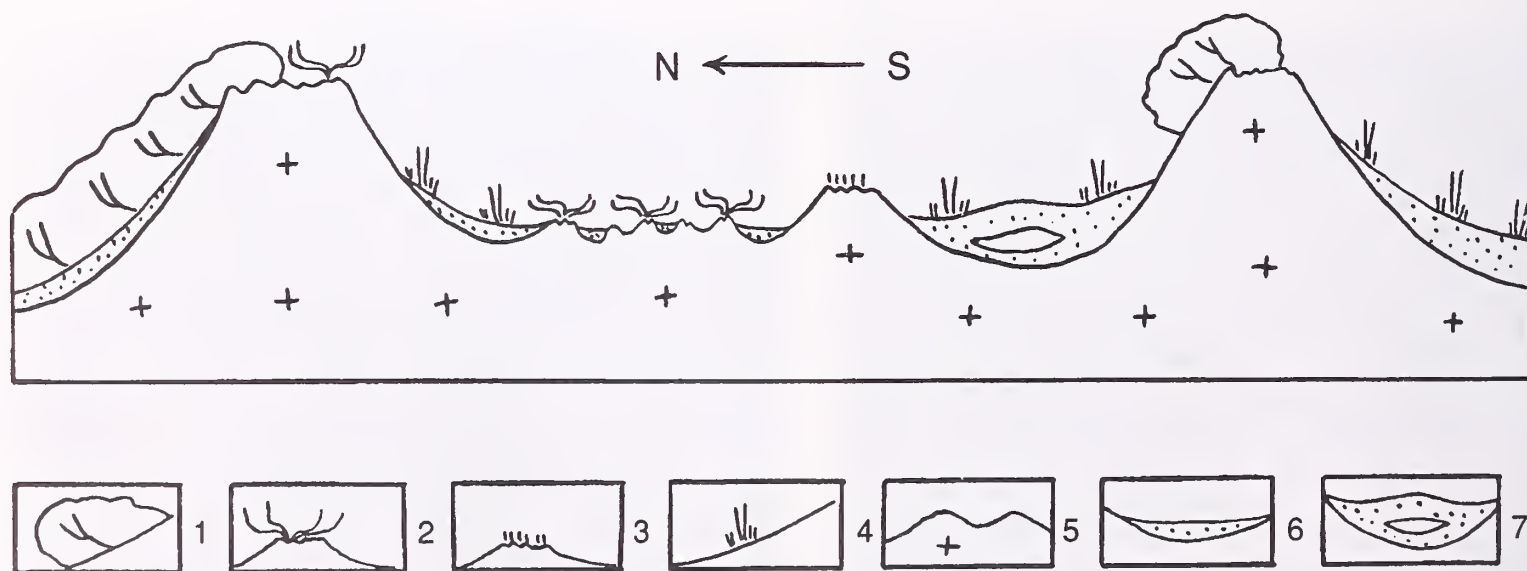


Figure 8—The distribution of vegetation across aa lava flow about 1,000 years old. 1—alder krummholz; 2—shrubs of *Pinus pumila*; 3—petrophilous alder groups in the lava outcrops; 4—bunches of grasses; 5—lava matter; 6—tephra of 1975; 7—buried snow patches.

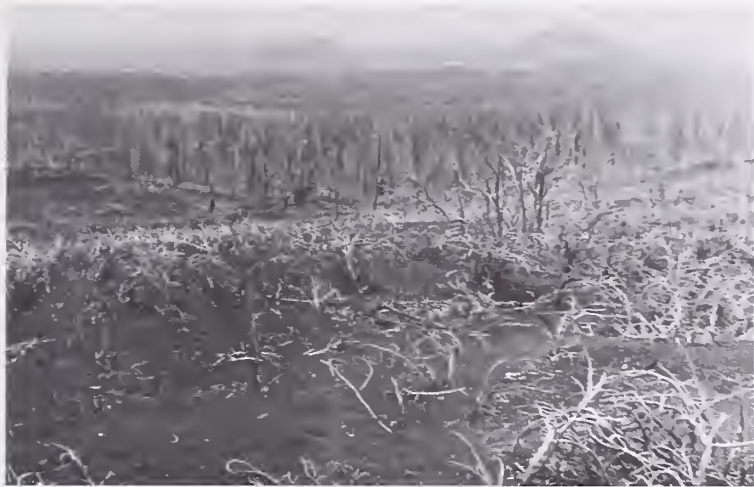


Figure 9—Timberline ecotone vegetation killed by ash fall on a lava flow that was about 2,000 years old.



Figure 10—Suppressed *Pinus pumila* and stunted trees of larch on pahoehoe lava about 1,000 years old.

cannot populate all the surface of the pahoehoe, and the next stages of succession are dependent on the space correlation between lithosere and psammosere. On aa lava this correlation changes to psammosere more quickly, and that accelerates succession. The final stages of succession on different types of lava are probably similar because a thick soil-tephra profile is gradually formed, smoothing out the irregularities of lava.

Another factor important to the succession rate is climate. In the area studied, the duration of succession is two to three times longer than in the oceanic climate of the Japanese subtropics, where it continues for only 700 years (Tagawa 1964).

A very important factor following volcanism is ash fall damage to vegetation. For example, in the Tolbachik area, about 10 eruptions took place during the last 2,000 years. Four of them were similar to the eruptions of 1975; in that period the tephra of volcanoes Shiveluch, Kluchevskoy, and

Bezmyanny were also deposited. The negative influence of major ash falls on vegetation was shown by the 1975 eruption. *Pinus pumila* krummholz and subalpine birch forests were killed under the tephra deposit of more than 20 cm, alder krummholz under more than 30 cm, and larch forests under more than 40 cm. Smaller amounts of tephra (10 to 15 cm) lead to the death of vegetation in subalpine meadows and alpine heaths. After moderate ash fall, a secondary succession is possible, and thus lithosere may be transformed to psammosere.

There are other essential factors of succession such as climatic fluctuations of forest and subalpine vegetation at their upper limit and forest fires. Fires may originate from volcanic eruption. Communities of coniferous trees (larch, spruce) and especially krummholz (*P. pumila*) with dry lichens and dwarf shrubs from *Ericaceae* are only slightly protected from fires.

Thus, the role of *P. pumila* in the succession on the lava flows of the Tolbachik area is different at different stages of succession. Because of its ecological and biological characteristics, it is not a pioneer at the initial stage. *Pinus pumila* plays its main role during the first half of succession (up to approximately 1,000 years). It forms closed communities and soil cover, and favors the establishment of dominant species in new communities of the subalpine zone. During the second half of succession, plant cover of *P. pumila* gradually decreases to the level typical of climax vegetation (fig. 11).

CONCLUDING REMARKS

On the whole, the role of *P. pumila* in succession is unique: It restores vegetation cover on juvenile substrate unfavorable for the establishment and development of woody and shrubby species. This feature of *P. pumila* is realized especially in the regions with continental climate. In places with oceanic climate, for example on the slopes of the Kluchevskoy volcano, the coniferous dominants *P. pumila* and *Larix*

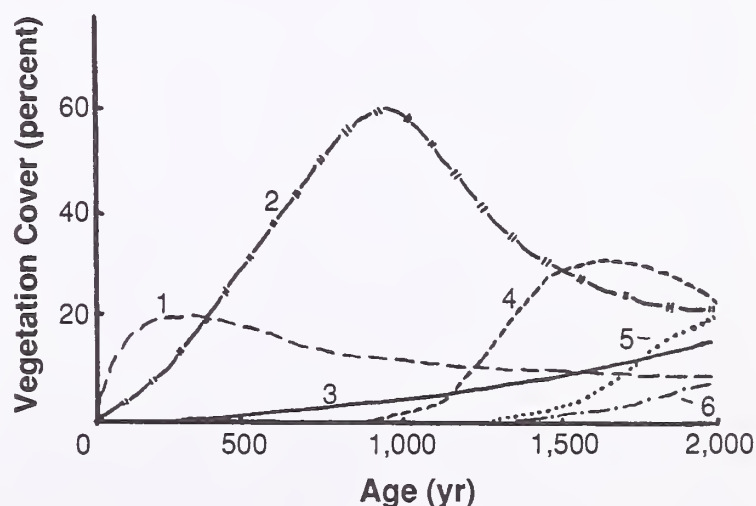


Figure 11—Generalized chronocline of succession on lava flows of the Tolbachik area. 1—pioneer unclosed groups of grasses, mosses, lichens; 2—communities of *Pinus pumila*; 3—woodlands of larch; 4—communities of alder krummholz; 5—birch forests; 6—subalpine meadows.

kamtschatica are replaced by deciduous species such as *Populus suaveolens*, *Duschekia kamtschatica*, and *Salix* spp. Nevertheless, *P. pumila* is widely distributed in the mountains of the volcanic island arc of the northwest Pacific (Kamchatka, Kurile, and Japan islands). *Pinus pumila* may probably be used to restore vegetation on eroded and rocky places in other high-mountain regions of the Northern Hemisphere.

REFERENCES

- Braitseva, O. A.; Melekescev, I. V.; Ponomariova, V. V.; and others. 1981. Tephrochronological and geochronological investigation of Tolbachik regional zone of scoria cones. *Volcanology and Seismology*. (2): 14-28. [In Russian].
- Czerepanov, S. K. 1981. *Plantae vasculares URSS*. Leningrad: Nauka. 510 p.
- Fedotov, S. A., ed. 1984. A major fissure Tolbachik eruption (1975-1976, Kamchatka). Moscow: Nauka. 638 p. [In Russian].
- Grishin, S. Yu. 1988a. The upper timberline at Kluchevskaya volcano group. In: Kharkevich S. S., resp. ed. *Plant cover of high-mountain ecosystems of the USSR*. Vladivostok: Far East Branch of Academy of Sciences of the USSR: 193-201. [In Russian].
- Grishin, S. Yu. 1988b. Structure of timberline ecotone vegetation on Mt. Dalnaya Ploskaya (Kamchatka). In: *Komarovskie chtenia, XXXV*. Vladivostok: Far East Branch of Academy of Sciences of the USSR: 159-175. [In Russian].
- Grishin, S. Yu. 1992. The successions of subalpine vegetation on the lava flows of Tolbachik area. *Botanical Journal [of Russian Botanical Society]*. 77(1): 92-100. [In Russian].
- Tagawa, H. 1964. A study of the volcanic vegetation in Sakurajima, South-West Japan. 1. Dynamics of vegetation. *Mem. Fac. Sci. Kyushu Univ. Ser. E(Bot.)*. 3(3-4): 165-228.

DECLINE OF WHITEBARK PINE IN THE BOB MARSHALL WILDERNESS COMPLEX OF MONTANA, U.S.A.

Robert E. Keane
Penelope Morgan

Abstract—Populations of whitebark pine (*Pinus albicaulis*) in the Northern Rocky Mountains, USA, are being reduced at alarming rates due to combined or individual effects of blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and advancing succession resulting from fire suppression. Results of an extensive field survey of various whitebark pine communities were used to evaluate past and current whitebark pine population levels. The ecological process model FIRESUM was then used to simulate forest succession with effects of blister rust and long-term fire suppression. Results indicate whitebark pine population levels are significantly decreasing, mostly as a result of blister rust, but decreases may be mitigated by the reintroduction of fire.

Whitebark pine (*Pinus albicaulis*) is a common tree species of Northern Rocky Mountain upper subalpine forests and timberlines. In Montana, Idaho, and northwestern Wyoming, USA, whitebark pine is an important component of about 10-15 percent of the forested landscape. Its slow growth, modest stature, and inaccessible habitats generally make it a low value commercial timber species. However, its cones are highly valued by many species of wildlife as a source of food. Animals that utilize whitebark pine cone crops include black and grizzly bears (*Ursus americanus* and *U. arctos horribilis*), red squirrels (*Tamiasciurus hudsonicus*) (Ferner 1974), and the Clark's nutcracker (*Nucifraga columbiana*) (Kendall 1980; Mattson and Reinhart 1986). The nutcracker plays an important mutualistic role in whitebark pine regeneration because it is essentially the only dispersal vector for whitebark pine seed (Tomback 1982; Tomback and others 1990). Whitebark pine is also important for snow retention and watershed protection in high-elevation areas where no other species can become established (Hann 1990).

Whitebark pine populations have been observed to be declining in parts of the Northern Rocky Mountains (Arno 1986; Ciesla and Furniss 1986; Kendall and Arno 1990; Moore 1984). The cause of the decline has been mainly attributed to mountain pine beetle (*Dendroctonus ponderosae*), successional advancement, and white pine

blister rust (*Cronartium ribicola*). Mountain pine beetle epidemics killed many whitebark pine trees during the early 1900's (Arno 1970; Arno and Hoff 1989). Extensive successional replacement of whitebark pine by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) may be a direct result of more than a half century of fire suppression (Arno 1986). The most damaging agent, blister rust, is an introduced disease that is especially devastating to whitebark pine (Arno and Hoff 1989; Bedwell and Childs 1943; Bingham 1972; Hoff and others 1980). Unfortunately, the extent and severity of whitebark pine decline is unknown in the Northern Rocky Mountains because documentation has been mostly from casual observations rather than scientific investigation.

This study was initiated to determine historical, current, and future whitebark pine population levels in a portion of the Northern Rocky Mountains known as the Bob Marshall Wilderness Complex. Whitebark pine communities were intensively inventoried throughout this study area. Community structure and age information were used to reconstruct historical community compositions. An ecosystem process model was used with sampled data to predict the future of these forests under four scenarios.

STUDY AREA

The Bob Marshall Wilderness Complex (BMWC) is a remote 600,000-hectare preserve in northwestern Montana, USA, composed of the Great Bear, Bob Marshall, and Scapegoat Wildernesses (fig. 1). This large area consists of mountainous terrain dissected by large river drainages. Parent material is mostly quartzite and argillite with alternating layers of limestone. The Continental Divide runs through the wilderness creating a unique blend of climates and plant communities. Climate west of the Divide is mostly maritime-continental with cool wet winters and warm dry summers. The east side climate is mostly continental with cold dry winters and warm dry summers.

Whitebark pine is a forest component above approximately 1,800 m in the study area. It has the potential to dominate 20-30 percent of the landscape within the entire study area (Bain 1989). Whitebark pine is seral to subalpine fir and Engelmann spruce in most of the area, but it can form climax stands on high, dry ridge and mountain tops.

Fire was a dominant process on the BMWC landscape. Ayers (1901) estimated 40 percent of BMWC's whitebark pine forests were burned between 1858 and 1898. Large, stand-replacement fires are typical in the study area, especially in the whitebark pine zone (Losensky 1990).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Robert E. Keane is Research Ecologist, Intermountain Fire Sciences Laboratory, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, P.O. Box 8089, Missoula, MT, USA 59801; Penelope Morgan is Professor of Fire Ecology, Department of Forest Resources, University of Idaho, Moscow, ID, USA 83843.



Figure 1—Bob Marshall Wilderness Complex in the west-central portion of Montana, USA, with locations of all whitebark pine sample sites across the complex shown by the "stars."

The great distances that nutcrackers transport seed allow whitebark pine a competitive advantage in colonizing vast burned areas (Tomback 1990). Clark's nutcrackers prefer open areas to cache whitebark pine seeds (Sund and others 1991). Some whitebark pine stands contain evidence of low-severity, frequent surface fires (Gabriel 1976). These fires kill many subalpine fir trees that compete with the more fire-resistant whitebark pine (Arno 1986).

MODEL DESCRIPTION

FIRESUM is a FORTRAN 77 computer model used to simulate important ecological processes in forested ecosystems. A complete description of FIRESUM is given in Keane and others (1989). In general, effects of shading, crowding, water availability, and climate on tree growth, regeneration, and mortality are simulated from stand structure, weather, and soils information. Trees die either from stress-induced mortality evaluated from the annual diameter increment, or from natural causes modeled from stochastic functions. Fires can kill trees, and they also reduce fuel loadings and duff/litter depths. Woody fuels are modeled empirically and used to compute fire intensity and spread rates. Duff and litter depths are simulated dynamically from litterfall and decomposition rates then used to reduce regeneration rates or promote fire spread.

Regeneration of wind-dispersed tree species is modeled stochastically in FIRESUM from the processes mentioned above and also from cone crop frequency, distance from seed source, and stand composition. However, since whitebark pine seeds are dispersed by the Clark's nutcracker, additional simulation algorithms were added to FIRESUM to account for Clark's nutcracker population levels, site suitability for seed caching, and cone availability. These algorithms are presented in Keane and others (1990a,b) and provide the means for modeling whitebark pine cone crops.

FIELD METHODS

Stand structure, fire history, fuels, site, and plant community information were sampled in various whitebark pine stands across the entire BMWC (Keane and others, in preparation). Trees were intensively sampled for age, size, and vigor within a 400-m² circular macroplot. Tree fire scars and tree ages were used to obtain a fire history (Arno and Sneek 1977). Down, dead woody fuels (twigs, branches, and logs) were inventoried around the macroplot using transect techniques (Brown 1974). ECODATA methods (Hann and others 1988; Keane and others 1990c) were used to record site information such as elevation, aspect, slope, and vascular plant community composition by species. Macroplots were located in a representative portion of whitebark pine stands and then accurately located using Global Positioning Systems (Hurn 1989) so the stand could be recognized from satellite imagery (Keane and others, in preparation).

Blister rust and mountain pine beetle evidence was recorded for each whitebark pine tree within the macroplot,

and also recorded for the entire stand. Blister rust severity was evaluated for each tree from (1) number of visible cankers per tree, (2) number of infected trees within the macroplot, and (3) amount of tree foliage killed by the rust. Causes of mortality were estimated for dead trees when evidence existed. When possible, snags and dead down trees were identified to species for historical stand reconstruction.

SIMULATION METHODS

FIRESUM was used to investigate effects of four ecological disturbance scenarios on tree species at the Cliff Mountain site, located in the central portion of the BMWC at 2,100 m elevation. Tree species input parameters to FIRESUM were taken from previous FIRESUM simulation exercises (Keane and others 1990a). Climate inputs were derived from weather data taken at a station just outside the BMWC boundary in the town of Seeley Lake. The model was calibrated with field data sampled from adjacent disturbed and mature whitebark pine communities on the Shale Mountain site, a sampled stand at 2,200 m on northwest aspect in south-central BMWC. The mature community tree data were used as initial stand condition inputs, and fire history of the disturbed community was used for disturbance input parameters to FIRESUM. Subsequent simulation results were compared to actual data from the disturbed community (Keane and others 1990a,b). As a result of these tests, model parameters and equations were adjusted to more closely approximate observed succession in these forests.

The following four scenarios were simulated in FIRESUM for the Cliff Mountain site over a 500-year period after parameter adjustment:

1. Fires at stochastic intervals averaging 150 years and no blister rust or beetle infestations.
2. No fires (complete fire suppression) with no blister rust or beetle infestations.
3. Blister rust infestation at year 100 and no fires.
4. Blister rust infestation at year 100 with 150-year stochastic interval fires.

Fire-free intervals of 150 years approximate historical fire frequency in most BMWC whitebark pine stands (Keane and others, in preparation). This stochastic interval implies there is a 0.0067 probability of a wildfire occurring in any simulation year. Predictions of species basal area, fire behavior, and fuel loadings were output from the model.

FIRESUM was then tested using stand structural data from adjacent postfire and mature stands for the Cliff Mountain and Tilison Mountain sampling sites. Tilison Mountain is located in the south-central portion of the BMWC near the Continental Divide. Both sites were burned in the 1910 fire that burned much of the BMWC. However, portions of the sites escaped the fire and stand data from these areas were used as inputs to the model. Observed conditions in the post-1910 stands were compared with FIRESUM predictions after 80 years of simulation.

Table 1—Average characteristics of whitebark pine stands types in the Bob Marshall Wilderness Complex

Tree species	Average percent overstory basal area ¹	Average overstory age ²	Average percent understory basal area	Average understory age
Whitebark pine	50	258	21	96
Subalpine fir	21	161	67	116
Engelmann spruce	16	228	6	101

¹Average percent of basal area by species in plots within each site type.

²Average age of each species in plots across each site type.

FIELD STUDY RESULTS

Summarized data from 106 sample sites (fig. 1) show whitebark pine stands consist of an overstory of old whitebark pine and younger subalpine fir and spruce with an understory of mostly subalpine fir and spruce (table 1). This is consistent with descriptions by Arno (1986) and Kendall and Arno (1990) to the effect that whitebark pine is being successional replaced by the more shade-tolerant fir and spruce. Downed woody fuels are scant (less than 5.5 kg/m²); most (approximately 5.0 kg/m²) are downed logs that decompose very slowly. Approximately 70 percent of down dead tree biomass is apparently whitebark pine.

Very little evidence of extensive mountain pine beetle epidemics was observed in the study area. Beetles seem to play the role of secondary colonizer, infecting already stressed pines and ultimately contributing to their death.

Evidence of blister rust was present in all but three of 106 sample stands. Blister rust infestation levels averaged around 80 percent with an average of 10 to 15 cankers per tree and 33 percent of tree foliage killed by the rust. Severity of blister rust infestations was related to geographic area but not correlated with topography or seral stage (table 2).

Blister rust is prevalent over the entire BMWC with the highest incidences observed in the northern and western portions of the study area (fig. 2a-c). Whitebark pine stands with the least number of cankers, portions of crown killed, and percents of trees infected appear to be in the southern end of the BMWC along the Continental Divide. Rust severity increases as one goes north, west, and east of the Continental Divide.

Fire history was difficult to determine in the BMWC because of the rarity of fire-scarred trees in the whitebark pine zone. It appears stand-replacement wildfires often burn trees that contain fire scars and leave few fire history records on the ground. However, an approximate fire history was determined from stand structure and the few fire scars found. The fire-free interval across all sample sites was approximately 144 years with a minimum of 55 and a maximum of 304 years (Keane and others, in preparation). Gabriel (1976) found that the Danaher drainage of the southern BMWC had an average stand-replacement fire rotation of 150 to 200 years. Stand age for all sample sites averaged approximately 250 years with less than 1 percent of these sites experiencing a fire in that time period.

Table 2—Bob Marshall Wilderness Complex blister rust severity by geographical area. General geographical boundaries are shown in figure 1 and are as follows: **Swan Front**—areas west of South Fork of Flathead River, **Continental Divide**—areas between South Fork Flathead River and North Fork Sun River and south of Middle Fork Flathead River, **Sawtooth Front**—areas east of North Fork Sun River, **Middle Fork**—areas in the Middle Fork Flathead River drainage (northern BMWC). Blister rust severity is expressed as a percent of total trees infected with rust, average number of cankers per tree, and percent of crown killed by rust

Geographical area	Number plots	Percent trees infected	Average cankers/tree	Percent crown kill
Swan Front	38	92	14	41*
Continental Divide	33	167*	9	15*
Sawtooth Front	17	86*	13	33*
Middle Fork	18	93	14	48*

* =significant at $p = 0.05$ using Kruskal-Wallis test within a rust severity measure.

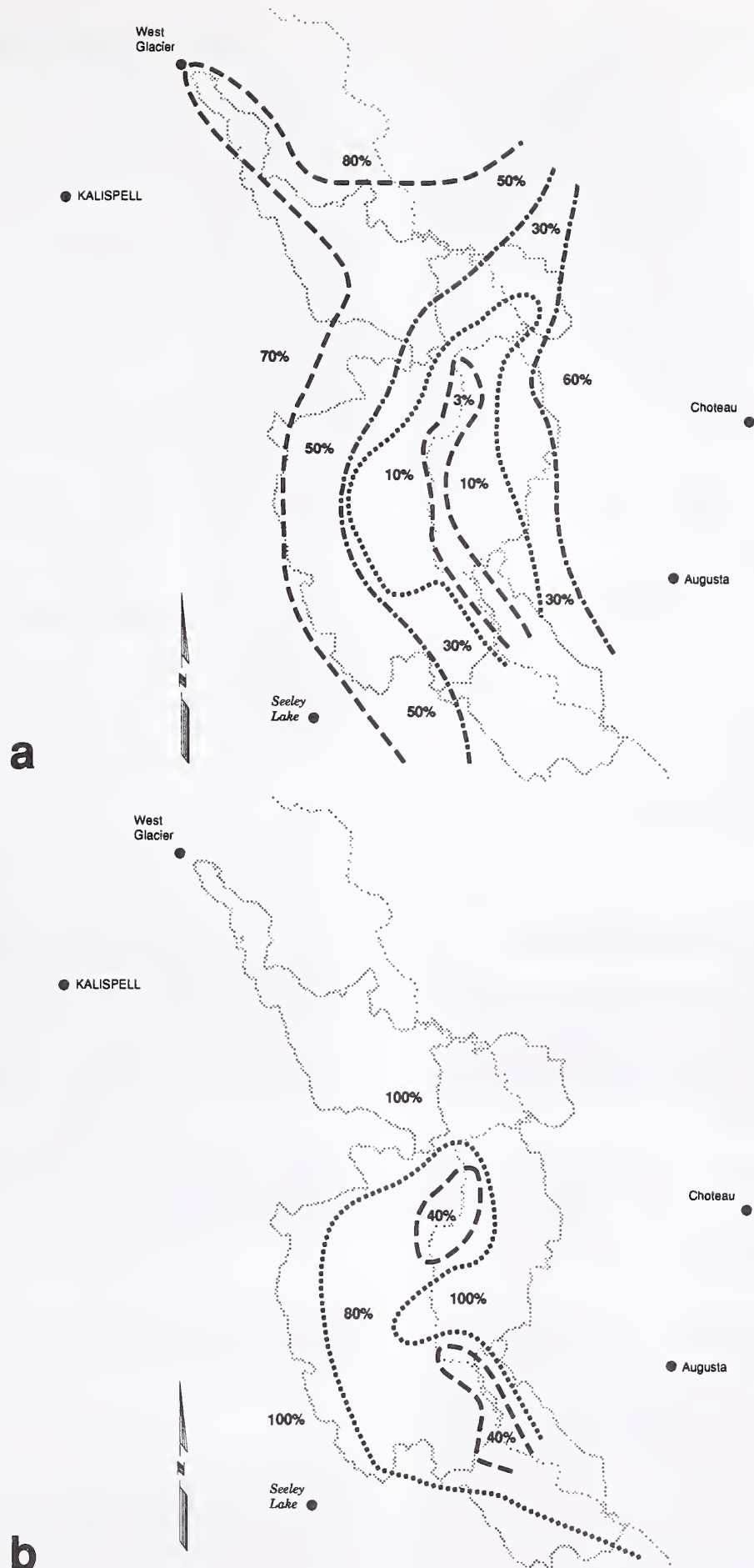


Figure 2—Isometric maps showing various levels of three measures of blister rust severity across the study area: a, blister rust infection levels (percent of trees infected by blister rust); b, blister rust canker levels (1: 1-5, 2: 5-10, 3: 10-15, 4: 16-20, 5: 21-25 cankers per tree); c, percent foliage killed by blister rust (estimated portion of live crown lost to blister rust).



Figure 2 (Con.)

SIMULATION STUDY RESULTS

FIRESUM testing results showed that the model performed moderately well in predicting successional stand composition. Predicted basal areas for whitebark pine and subalpine fir after 80 years of simulation were within about 20 to 30 percent of those observed in the actual post-1910 fire stands.

Whitebark pine stand dynamics differed greatly across the four modeling scenarios. Predicted whitebark pine (PIAL) basal area remained somewhat constant under a stochastic, 150-year historical fire regime with subalpine fir (ABLA) and Engelmann spruce (PIEN) present, but at lower levels (fig. 3a). However, whitebark pine basal area tended to decrease somewhat in the absence of fires while subalpine fir doubled its basal area (fig. 3b). Whitebark pine decline is greatly accelerated by blister rust infestations in the absence of fires (fig. 3c). Last, fire does not seem to affect the decrease in whitebark pine levels after blister rust introduction (fig. 3d).

DISCUSSION

Historical BMWC upper subalpine stands were most likely dominated by whitebark pine with a small component of fir and spruce. Presence of an older age class of whitebark pine (table 1), and the preponderance of whitebark pine snags (table 3) and downed logs, indicate that these stands once supported about 20-30 m²/ha of whitebark pine and very little spruce and fir.

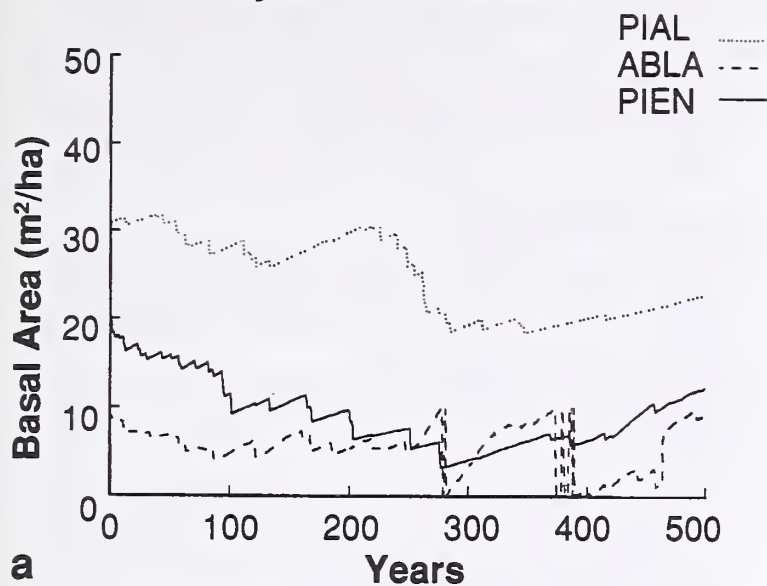
At present, whitebark pine is rapidly declining throughout most of the BMWC. Blister rust is killing many whitebark pine trees along the western, eastern, and northern boundaries (fig. 2a-c). A 1991 remeasurement of whitebark pine trees in 1971 vegetation classification plots indicated that approximately 20 percent of the species' basal area and 30 percent of its trees are lost each decade due to blister rust (Keane and Arno 1993). Absence of whitebark regeneration in sample macroplots (table 1) indicated fir and spruce will eventually replace whitebark pine without fire.

Lack of fire on the landscape has allowed subalpine fir and Engelmann spruce to dominate the understory of forests previously dominated mostly by whitebark pine (table 1). As a result of fire suppression, few subalpine areas have been opened by fire for nutcracker dispersal

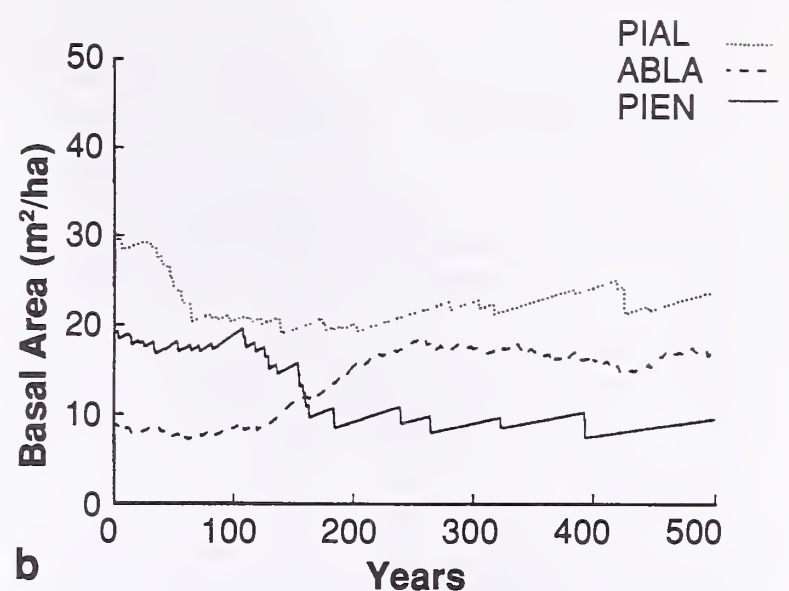
Table 3—Standing live and dead tree densities (trees/ha) by species for whitebark pine stands in the Bob Marshall Wilderness Complex

Tree species	Live tree density	Live tree basal area	Dead tree density	Dead tree basal area
	Trees/ha	m ² /ha	Trees/ha	m ² /ha
Whitebark pine	218	15.0	43	5.2
Subalpine fir	490	5.3	23	3.7
Engelmann spruce	61	5.7	2	.4

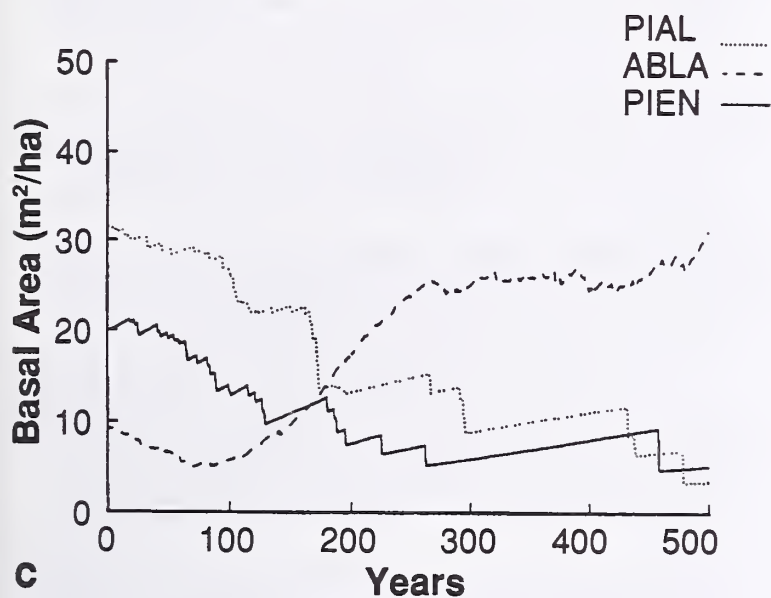
150-year Fire Interval



No Fire



Blister Rust



Blister Rust/Fire

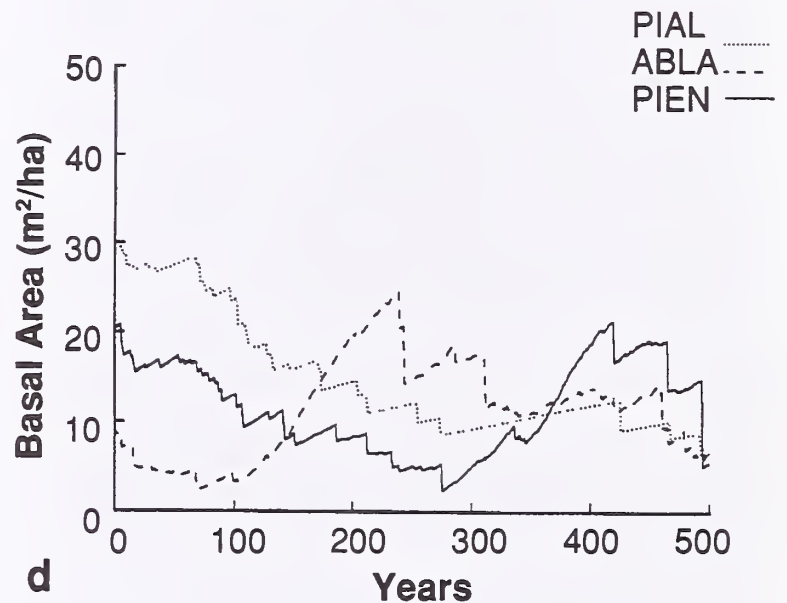


Figure 3—FIRESUM simulation results for Cliff Mountain site under the four modeling scenarios: a, 150-year stochastic fire regime; b, no fires (fire suppression); c, blister rust infection at year 100; d, 150-year stochastic fire regime and blister rust infection at year 100.

of whitebark pine seeds. Most sampled stands were older (>250 years) than the estimated fire return interval (144 years) indicating that a majority of whitebark pine stands have exceeded the expected fire rotation.

Fires were an important disturbance on the BMWC landscape. Extensive, stand-replacement fires such as those documented by Ayers (1901) created burned areas colonized by whitebark pine seedlings from nutcracker-cached seed. These large fires often occurred in heavy fuels during extreme dry, windy weather conditions (Losensky 1990). Fires started in subalpine areas during moderate weather years consumed scattered surface fuels and often did not ignite tree crowns. However, these surface fires generally killed fire-intolerant fir, spruce, and young whitebark, but only scarred the older, large

whitebark pine trees. This type of fire regime created open, parklike stands of nearly pure whitebark pine (Arno 1986).

Model results show that future BMWC subalpine forests will probably be composed mostly of fir and spruce with little whitebark pine (fig. 3c-d). Introduction of fire into the BMWC may not accelerate the loss of the species at the stand level, but may help perpetuate the presence of whitebark pine on the BMWC landscape level because burned-over areas are better nutcracker caching sites. Data summaries of whitebark pine classification plot remeasurements (Keane and Arno 1993) agree with FIRESUM modeling results that predict severe reduction in whitebark pine densities 40-50 years after blister rust introduction (fig. 3c).

CONCLUSIONS

Whitebark pine populations in the BMWC are decreasing at an alarming rate. Most stands will probably be converted to dense subalpine fir and spruce with minor components of whitebark pine. However, cold, dry sites where whitebark pine is the indicated climax may be converted to shrub or herbaceous communities; this may adversely affect snow retention and watershed dynamics (Keane and others 1990b). Areas currently with low levels of blister rust (such as the southern end of the Continental Divide) will probably also experience heavy whitebark pine mortality, though much more slowly than other regions due to more infrequent weather conditions conducive to blister rust infection and growth (Hagle and others 1989).

Results of this study could be extrapolated to other parts of whitebark pine's range that experience similar weather patterns. Whitebark pine population levels in Glacier National Park, USA, have decreased drastically in the last 20 years (Kendall and Arno 1980) due mainly to blister rust. Arno (1986) observed a decline in whitebark pine in the Bitterroot Range of Montana and Idaho, USA. Blister rust has been documented in the southern portions of whitebark pine's range, but the mortality has not been as extensive, presumably due to drier weather conditions (Carson 1978). However, given suitable weather conditions, blister rust may infect many more trees in this drier portion of its range.

Reduction of whitebark pine cone crops could affect many species of wildlife. Grizzly and black bears must either migrate or find a new source of prehibernation foodstuffs (Craighead and others 1982; Kendall 1980; Mattson and Reinhart 1986). Squirrels and Clark's nutcrackers will also need to find alternate food sources, as will other animals dependent on them. Shifts in vegetation composition and wildlife migration can cause major changes in landscape diversity and structure. In turn, this may affect the pattern of fire processes.

About 1 to 8 percent of whitebark pine populations may be genetically resistant to blister rust (Arno and Hoff 1989; Bingham 1972; Hoff and others 1980). This might allow whitebark pine to remain on the landscape at very low levels. However, the combined effects of blister rust and successional replacement due to fire suppression will make it impossible to maintain current whitebark pine population levels even with high rust resistance. Also, if these populations become very small, nutcracker seed consumption during late summer could destroy most of the seed crop (Tomback 1982). Breeding rust-resistant populations will be important for maintaining whitebark pine in the critical portions of its range, especially where it is currently a major food for the grizzly bear. Encouraging nutcracker caching by opening dense stands with fire may also promote whitebark pine populations (Sund and others 1991).

ACKNOWLEDGMENTS

The authors thank personnel of the Spotted Bear District of the Flathead National Forest and the Rocky

Mountain District of the Lewis and Clark National Forest for all the aid and assistance offered throughout the project. Thanks to James Menakis and Steve Arno of the Intermountain Research Station for their unlimited help; and Wendel Hann of Forest Service, Northern Region, Ecology for his never-ending support.

REFERENCES

- Arno, S. F. 1970. Ecology of alpine larch (*Larix lyallii*) in the Pacific Northwest. Missoula, MT: University of Montana. 264 p. Dissertation.
- Arno, S. F. 1986. Whitebark pine cone crops: a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-94.
- Arno, S. F.; Hoff, R. J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.
- Arno, S. F.; Sneek, K. M. 1977. A method for determining fire history in coniferous forests of the Mountain West. Gen. Tech. Rep. INT-42. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 28 p.
- Ayres, H. B. 1901. Lewis and Clark forest reserve, Montana. 21st Annual Report. Part 5. Washington, DC: U.S. Department of the Interior, Geological Survey: 27-80.
- Bain, S. 1989. LANDSAT classification and field correlation methods for vegetation classification used at the Flathead National Forest. In: Ferguson, D. E.; Morgan, P.; Johnson, F. D., comps. Proceedings—land classification based on vegetation: applications for resource management; 1987 November 17-19; Moscow, ID. Gen. Tech. Rep. INT-257. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 255-258.
- Bedwell, J. L.; Childs, T. W. 1943. Susceptibility of whitebark pine to blister rust in the Pacific Northwest. *Journal of Forestry*. 41: 904-912.
- Bingham, R. T. 1972. Taxonomy, crossability, and relative blister rust resistance of 5-needled white pines. In: Biology of rust resistance in forest trees. Misc. Publ. 1221. Washington, DC: U.S. Department of Agriculture, Forest Service: 271-280.
- Brown, James K. 1974. Handbook for inventorying downed woody fuel. Gen. Tech. Rep. INT-16. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 24 p.
- Carlson, C. E. 1978. Noneffectiveness of *Ribes* eradication as a control of white pine blister rust in Yellowstone National Park. Forest Insect and Disease Mgmt. Rep. 78-18. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 6 p.
- Ciesla, W. M.; Furniss, M. M. 1986. Idaho's haunted forests. *American Forests*. 81(8): 32-35.
- Craighead, J. J.; Summer, J. S.; Scaggs, G. B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources utilizing LANDSAT multispectral imagery and computer technology. Wildlife-Wildlands Inst. Monogr. 1. Missoula, MT: University of Montana Foundation, University of Montana. 279 p.

- Ferner, J. W. 1974. Habitat relationships of *Tamiasciurus hudsonicus* and *Sciurus aberti* in the Rocky Mountains. *Southwest Naturalist*. 18: 470-473.
- Gabriel, H. W. 1976. Wilderness ecology: the Danaher Creek drainage, Bob Marshall Wilderness, Montana. Missoula, MT: University of Montana. 224 p. Thesis.
- Hagle, S. K.; McDonald, G. I.; Norby, E. A. 1989. White pine blister rust in northern Idaho and western Montana: alternatives for integrated management. Gen. Tech. Rep. INT-261. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 35 p.
- Hann, W. J. 1990. Landscape ecology and vegetation management in whitebark pine ecosystems. In: Proceedings of the symposium—whitebark pine ecosystems: ecology and management of a high mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 335-340.
- Hann, W. J.; Jensen, M. E.; Keane, R. E. 1988. Chapter 4: Ecosystem management handbook—ECODATA methods and field forms. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Northern Region, Missoula, MT. 75 p.
- Hoff, R.; Bingham, R.; McDonald, G. J. 1980. Relative blister rust resistance of white pines. *European Journal of Forest Pathology*. 10: 307-316.
- Hoff, R. J.; McDonald, G. I. 1977. Different susceptibility of 19 white pine species to woolly aphid (*Pineus coloradensis*). Res. Note INT-225. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 4 p.
- Hurn, J. 1989. GPS—a guide to the next utility. Sunnyvale, CA: Trimble Navigation. 76 p.
- Keane, R. E.; Arno, S. F. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year measurements. *Western Journal of Applied Forestry*. [In press].
- Keane, R. E.; Arno, S. F.; Brown, J. K. 1989. FIRESUM—an ecological process model for fire succession in western conifer forests. Gen. Tech. Rep. INT-266. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 76 p.
- Keane, R. E.; Arno, S. F.; Brown, J. K.; Tomback, D. F. 1990a. Modelling stand dynamics in whitebark pine forests. *Ecological Modelling*. 51: 73-95.
- Keane, R. E.; Arno, S. F.; Brown, J. K. 1990b. Modeling disturbance and conifer succession in whitebark pine forest. In: Proceedings of the symposium—whitebark pine ecosystems: ecology and management of a high mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 274-289.
- Keane, R. E.; Jensen, M. E.; Hann, W. J. 1990c. ECODATA and ECOPAC—analytical tools for integrated resource management. *The Compiler*. 8(3): 24-37.
- Keane, R. E.; Morgan, P.; Menakis, J. [In preparation]. Status of whitebark pine (*Pinus albicaulis*) on the Bob Marshall Wilderness Complex landscape.
- Kendall, K. C. 1980. Bear-squirrel-pine nut interaction. In: Yellowstone grizzly bear investigations. Annual Report 1978-1979. West Glacier, MT: U.S. Department of the Interior, National Park Service: 51-60.
- Kendall, K. C.; Arno, S. F. 1990. Whitebark pine—an important but endangered wildlife resource. In: Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 264-274.
- Losensky, J. 1990. A comparison of the 1988 fire season to the historical role of fire for the Bob Marshall-Great Bear-Scapegoat wilderness complex. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, Missoula, MT. 22 p.
- Mattson, D. J.; Reinhart, D. P. 1986. Grizzly bear, red squirrels, and whitebark pine: second year progress report. Report submitted to Interagency Grizzly Bear Study Team. Bozeman, MT: U.S. Fish and Wildlife Service. 38 p.
- Moore, W. R. 1984. Last of the Bitterroot grizzly. *Montana Magazine*. 68: 8-12.
- Sund, S. K.; Tomback, D. F.; Hoffman, L. 1991. Post-fire regeneration of *Pinus albicaulis* in western Montana: patterns of occurrence and site characteristics. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, Missoula, MT. 55 p.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. *Journal of Animal Ecology*. 51: 451-467.
- Tomback, D. F.; Hoffman, L. A.; Sund, S. K. 1990. Coevolution of whitebark pine and nutcrackers: implications for forest regeneration. In: Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 118-130.

SOME ASPECTS OF CEMBRAN PINE REGENERATION IN THE ITALIAN COTTIAN ALPS

Renzo Motta
Alberto Dotta

Abstract—In the Susa, Chisone, and Varaita Valleys a spontaneous diffusion of cembran pine (*Pinus cembra*) has been observed during the last few decades in various types of environments and at altitudes between 1,100 and 2,850 m. The initial height growth of this species is very slow. A mean age of 44 years at a height of 120 cm was found in 86 cembran pines taken from 10 different sites. Regeneration does not show serious problems that could be attributed to the influences of fungi and insects or climatic factors. The main cause of death is the damage caused by game, in particular fraying damage caused by red deer (*Capreolus capreolus*) and roe deer (*Cervus elaphus*).

In the western Italian Alps the cembran pine (*Pinus cembra*) covers a limited area compared to its potential natural range. The reasons behind this are well known (Filipello and others 1976; Stern 1988) and may be summarized as follows:

- replacement of woodland by grazing and timberline depression;
- replacement of cembran pine by other species, in particular larch (*Larix decidua*), which is more suitable for multiple-use forestry—particularly for livestock grazing;
- over-exploitation.

In the wake of the profound socio-economic change that has occurred during the last few decades, human activity in the alpine valleys has also radically changed. Decline of forest use and grazing has allowed a widespread, spontaneous regeneration of cembran pine.

The aim of this study is to describe the main environments in which this widespread regeneration has taken place, to observe the speed with which this process has come about by analyzing the early height growth of this pine (up to the height of 120 cm), to determine the influence of the direct sunlight on the increasing regeneration, and to highlight the major problems with regeneration during this initial stage of secondary succession.

CEMBRAN PINE DISTRIBUTION

The regional distribution of cembran pine is, in broad perspectives, quite well known (Bono and Barbero 1971; Hoffman 1970). The southern limit of the species in Piedmont, and indeed over the entire mountain range, is located on the slopes of Mount Mongioie in the Tanaro Valley at an altitude of 1,800 m above sea level on a southern exposure. Proceeding northward, cembran pine occurs sporadically in the Pesio Valley and more frequently, although generally concentrated in rocky sites, in the Gesso, Stura, and Maira Valleys. Cembran pine is well represented in the Varaita, Chisone, and Susa Valleys.

The presence of cembran pine in the more northerly sector of the region is limited. In the Insubric region it is almost absent for climatic reasons, in the Sesia Valley only a small spontaneous population is found in the Vogna Valley (Bertolani-Marchetti 1961), while there are two populations in the Ossola Valleys: one in the Anzasca Valley and another one in the Formazza Valley (Tiraboschi 1964). However, in this latter area old tree stumps, beams used for roofs, and trunks found in the mountain lakes could lead one to suppose that cembran pine was present in the past in areas where it is no longer to be found (Falcini 1989).

Altogether, in Piedmont pure cembran pine forest occupies an acreage of approximately 1,500 ha while mixed forest amounts to over 3,500 ha (Regione Piemonte, Ipla 1985). The majority of this forest area (over 60 percent) is, however, concentrated in three valleys of the Cottian Alps that have been the subject of our observations: the Varaita, Chisone, and Susa Valleys (fig. 1).

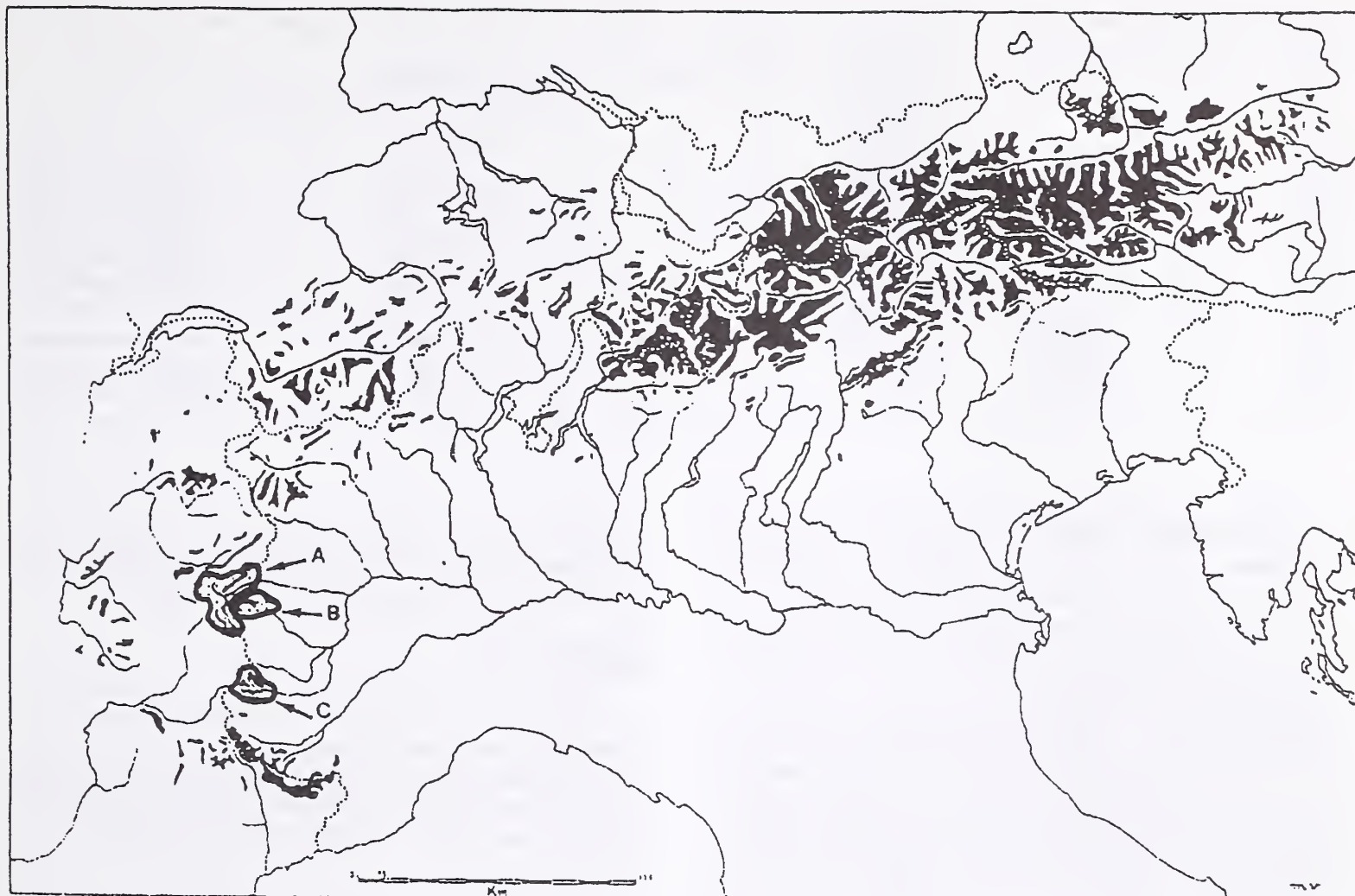
STUDY AREA

Toward the end of the Susa and Chisone Valleys, several kinds of geological substratum can be observed: Calcschists are most common but also quartzite, gneiss, mica schist, serpentine, and limestone are represented. The Varaita Valley is characterized mainly by metamorphic rocks (gneiss, quartzite, mica schist), Monviso diabases, and by a wide belt of calcschists.

Susa and Chisone Valleys are dry areas and belong to the most continental region in the Alps (Richard and Tonnel 1987). At some sites, annual precipitation is less than 700 mm. Rainfall regime is of Piedmont equinoxial type with maxima in spring (the principal) and in autumn. Winter is the driest season. In the Varaita Valley precipitation is more uniform throughout the year, and annual precipitation is 760 to 1,300 mm.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Renzo Motta, Dipartimento di Agronomia Selvicoltura e Gestione del Territorio, Università degli Studi di Torino. Via L. Da Vinci 44, Grugliasco (TO), I 10095; Alberto Dotta, Consorzio Forestale Alta Valle di Susa. P.zza Mistral 7, Oulx (TO), I 10056




- A - Upper Susa Valley
- B - Upper Chisone Valley
- C - Upper Varaita Valley
-  Cembran pine distribution in the Alps

Figure 1—Geographical distribution of cembran pine in the Alps and localization of the study sites (Filipello and others 1976; modified).

In the inner part of Susa and Chisone Valleys, the most-represented forest species is the larch. Among the other species, mostly in the Susa Valley, Scots pine (*Pinus sylvestris*), silver fir (*Abies alba*), and spruce (*Picea abies*) occur. Cembran pine forms a few small pure stands, especially close to the upper forest limit, which in Susa Valley is located above 2,400 m. In these two valleys there are also, in some special edaphic conditions, Swiss mountain pine (*Pinus uncinata*) stands. Larch is also the most common species in the Varaita Valley, extending down to lower elevations where it replaces beech (*Fagus sylvatica*) or is mixed with beech copses or mixed broad-leaved forests. Cembran pine can be either pure stands (southern aspects as Alevé forest) or mixed with larch stands (cooler aspects).

METHODS

Sampling on sample plots (table 1) at regular distances (1.5 km) along the contour lines of 1,500, 1,700, 1,900, and 2,100 m (according to "3P" method) allowed us to describe sites and cembran pine regeneration in the areas examined and to identify the environments preferred for regeneration.

We were able to identify 106 areas in the Susa Valley, 31 in the Chisone Valley, and 34 in the Varaita Valley. In each of these areas we have analyzed the main characteristics of the site (aspect, gradient, geology, vegetation) and of the forest (species, height, health, damages).

Other research has been carried out at tree limit and the upper regeneration limit of the cembran pine (Piussi

Table 1—Description of sample plots

Valley	Site	Altitude	Aspect	Geology	Vegetation
		Meters			
Varaita	Alevé 1	1,800	S-W	Ophiolite	Cembran pine stand
Varaita	Alevé 1	2,200	S-W	Ophiolite	Cembran pine stand
Chisone	Souch. 1	1,500	N	Calcschist	Mountain larch stand
Chisone	Souch. 2	1,900	N	Calcschist	Subalpine larch stand
Chisone	Souch. 3	2,250	N	Calcschist	Subalpine larch stand
Susa	Enfer	1,800	E	Calcschist	Subalpine larch stand
Susa	M. Luna	2,100	W	Serpentine	Subalpine larch stand
Susa	P. Bosco	2,050	N-W	Calcschist	Cembran pine stand
Susa	Ruine	2,000	N-W	Calcschist	Subalpine larch stand
Susa	V. Gimont	2,150	W	Moraine	Subalpine larch stand

and Schneider 1985). Additional research has been conducted below 1,500 m in the montane forests to identify the lower altitudinal limit of distribution and regeneration.

Eight to 10 samples of cembran pine (height at least 120 cm) were taken at 10 sites that had been delineated by altitude and vegetation.

Trees of "average" growth form were chosen. These were growing either singly or in small clusters of two to four individuals in areas where regeneration was abundant. For the small clusters, a single tree per group was selected, which represented average habitat features and looked relatively undisturbed by the other cluster trees as far as the amount of sunlight received is concerned.

These sample trees were cut at the soil surface and then sectioned every 10 cm. The diameter of each section was measured and the annual rings counted.

RESULTS

In general, cembran pine regeneration is increasing considerably at present (fig. 2).

In broad terms, three types of environment can be distinguished in which cembran pine regeneration is spreading at present. These are outlined below in order of importance.

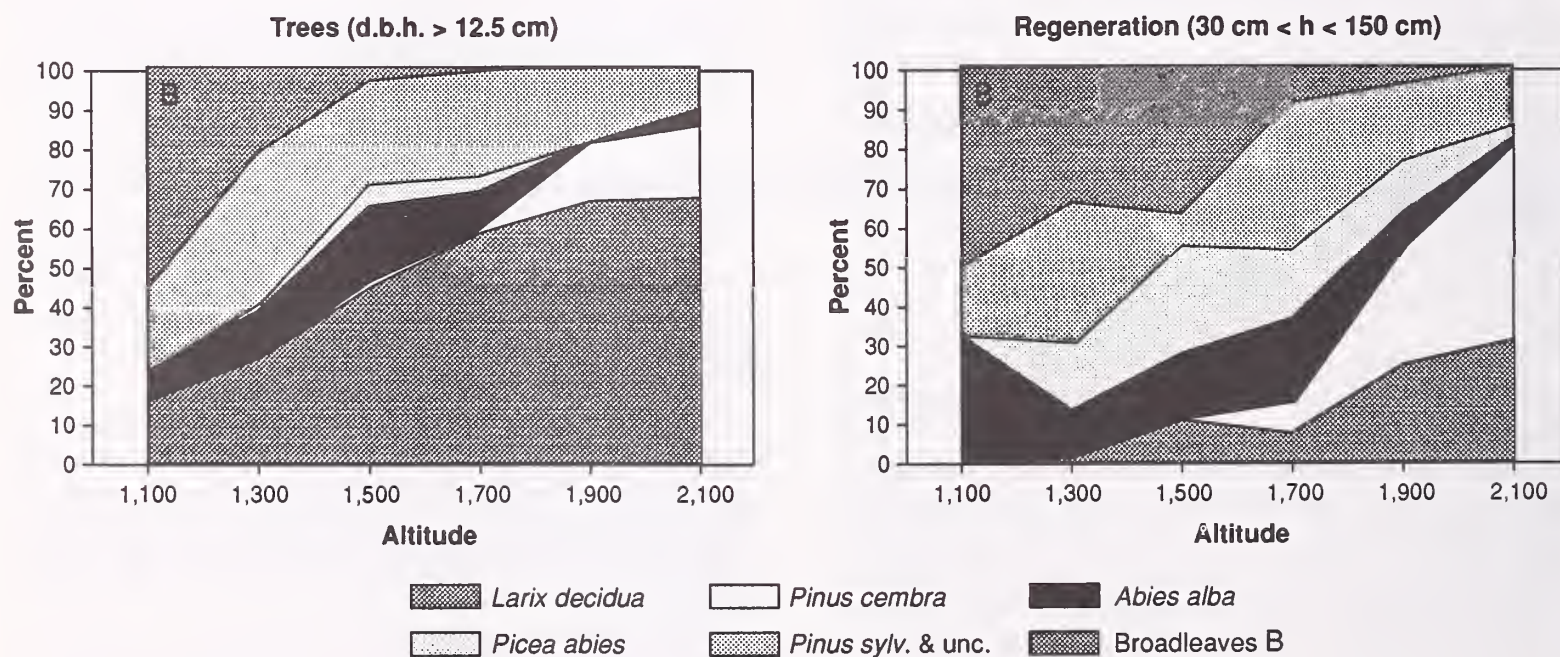


Figure 2—Percentage composition of trees (d.b.h. > 12.5 cm) and of regeneration (30 cm < h < 150 cm) at different altitudes in the Upper Susa Valley.

Woodland and Abandoned Pasture Land

Cembran pine is gradually invading areas again that were cleared by humans in the past. Cembran pine regeneration is very common, in particular under larch cover (Motta and Dotta 1992).

This phenomenon may also be favored by the thick layer of herbaceous vegetation on the larch forest floor, which prevents the seeds of other species from reaching the mineral soil. Seeds of cembran pine, thanks to the action of the nutcracker (*Nucifraga caryocatactes*), manage to overcome this obstacle. Furthermore, in these populations, seeds of cembran pine are stronger than seeds of other conifers because of comparatively high nutrient reserves. Therefore, seedlings of cembran pine can more easily compete with the herbaceous vegetation on the forest floor (Trepp 1981).

This process is generally more apparent on northern aspects, while on the southern aspects there are big differences between the three valleys.

In the Varaita Valley, the cembran pine forest of Alevé (from "elvù," cembran pine) occurs primarily on the southern exposure. In this valley cembran pine also is regenerating under the cover of larch stands, both on southern and on northern slopes.

This situation is in sharp contrast to those in the Susa and Chisone Valleys, where regeneration of cembran pine is predominant on northern slopes. The presence of cembran pine on the southern slope of the Chisone Valley of the hamlet "Alleve" within the municipality of Pragelato (approximately 1,800 m above sea level with an exposure very similar to that of Alevé in the Varaita Valley) seems to point to the fact that present absence of the cembran pine on the southern slopes of the upper Chisone Valley is likely due to the action of humans.

In the Susa Valley cembran pine's establishment on southern aspects is limited by ecological factors (Giordano and others 1974) and also by geological factors: On southern aspects serpentine, quartzite, and limestone are very common. These substrata are mainly colonized by *Pinus uncinata*.

Generally, southern slopes have likely been used for agriculture and grazing more intensely and for longer periods of time than northern slopes. Furthermore, the natural recolonization of these slopes is more difficult than it is on the northern slopes. Actually, cembran pine forests found on the southern slopes show a remarkable stability when conditions are suitable for regeneration (Beguín and Theurillat 1982), but as soon as they are disturbed they reveal a low resilience, and spontaneous recolonization of the original sites appears to be rather difficult.

Forest Limit and Ridges

At the forest limit cembran pine is reinvading ground where it had been excluded.

Cembran pine regeneration is also expanding on ridges and in isolated "gruppe" (clusters) that originated from seed caches of the nutcracker and are growing well above the vegetation limits. These constitute particularly favorable microsites, even though located within the alpine zone (Ozenda 1985). In the Susa, in the Chisone, and

Table 2—Upper altitude limits attained by cembra pine regeneration

Valley	Site	Tree limit	Forest limit	Aspect
----- Meters -----				
Varaita	Rocca Jarea	2,750	2,300	S-W
Varaita	Reisasso	2,680	2,380	S
Varaita	Roccio Russo	2,640	2,350	S
Varaita	Losetta	2,810	2,240	S
Varaita	Tre Chiois	2,800	2,150	S
Chisone	C. Chardonnnet	2,550	2,250	N-W
Chisone	Albergian	2,500	2,290	N-W
Susa	Dormilleuse	2,620	2,460	E
Susa	M. Gimont	2,620	2,400	E

in the Varaita Valleys the forest limits reach altitudes (table 2) among the highest of the entire Alps (above 2,400 m).

Montane Forests

This type of expansion (table 3) is less frequent compared with the two described earlier. It is present sporadically, however, in all three of the valleys examined in this study where regeneration of the cembran pine occurs at high altitudes and in uncommon forest types.

This phenomenon is by no means easy to interpret and cannot be considered separately from seed dispersal by the nutcracker (Mattes 1982). Certainly, because of the thick and dense herbaceous cover, cembran pine seeds have distinct advantages over those of other conifers, as was mentioned in the discussion of the subalpine zone.

Early Height Growth

A survey of the number of years young cembran pines need to grow to 120 cm in height has been carried out in order to know the duration of this first colonization period.

Analysis of the early height growth of cembran pines has already been conducted in other areas of the Alps (Contini and Lavarello 1982; Oswald 1963; Unterrichter 1986) by different authors using various methodologies. Some investigations carried out in the Upper Susa Valley

Table 3—Lower altitude limits attained by cembra pine regeneration in the montane zone

Valley	Site	Vegetation	Altitude	Aspect
Meters				
Varaita	Confine	Mountain larch stand	1,150	N
Varaita	Torrette	Beech stand	1,250	N
Chisone	Souch. basses	Mountain larch stand	1,450	N-W
Chisone	Fraisse	Mountain larch stand	1,480	N-W
Susa	Meana	Mountain larch stand	1,200	N
Susa	Mian	Beech-fir stand	1,250	N
Susa	Gran Bosco	Fir stand	1,300	N-E

Table 4—Number of years required to reach 120 cm height

Site	Number of trees	Mean age at 120 cm height	Age range	Standard deviation
a) Alevé 1	9	43	28-71	15.1
b) Alevé 2	8	45	38-51	4.7
c) Souch. 1	8	52	36-73	11.2
d) Souch. 2	8	59	49-68	6.7
e) Souch. 3	8	40	33-47	3.9
f) Enfer	8	39	35-44	2.9
g) M. Luna	9	55	36-77	10.0
h) V. Gimont	9	37	26-66	11.2
i) Ruine	9	39	26-49	7.6
l) P. Bosco	10	32	24-45	5.8
Varaita V. (a,b)	17	44	28-71	11.2
Chisone V. (c-e)	24	50	33-73	11.2
Susa V. (g-l)	45	40	24-77	11.2
Total	86	44	24-77	12.2

have, however, provided data significantly different from those published in literature. At the same time, the presence of cembran pine regeneration in such different situations as far as altitude, aspect, and type of vegetation are concerned has led us to proceed further with this line of research to see whether there are significant differences in the early height growth of the cembran pine under different ecological conditions.

From data collected, early growth appears to be significantly slower than observed by other authors (table 4).

In the Varaita Valley, the age of young cembran pine at 120 cm height is quite regular over the whole slope. However, growth rates slightly decrease with increasing altitude.

The situation in the Chisone Valley is the most interesting. Three sites were chosen of the same slope, aspect, geology, and vegetation (larch stands), but at different altitudes. The site at the highest altitude shows the best growth rates. Probably the competition of the abundant herbaceous vegetation on the two lower sites reduced the growth of cembran pines in the early decades of their life.

In the Susa Valley, cembran pines grow more quickly than in the other two valleys, with the exception of the area of Monti della Luna. There, the geological substratum (serpentine) and the shallow soil impede the growth of plants throughout their life.

Regeneration Problems

The Susa, Chisone, and Varaita Valleys are characterized by moderate winter snowfalls and early snow melt in spring. Consequently, problems related to *Phacidium infestans* and *Herpotrichia nigra* are negligible. In the Susa Valley, the endemic *Peridermium strobi* does not have any effect on adult plants, but may cause young trees to wilt and lead to higher mortality among seedlings. Also, problems caused by insects (in particular *Ips cembrae*) and frost damage are negligible. In the Varaita Valley, three fires have destroyed several hectares of cembran pine woodland during the last few decades, but these areas have promptly been recolonized by cembran pine.

The biggest problem regarding regeneration of the cembran pine is, at present, damage caused by wildlife (fig. 3). This damage is not distributed uniformly over the area. It is serious in the Susa Valley (28.9 percent of cembran pine regeneration damaged), substantial in the Chisone Valley (11.8 percent), and negligible in the Varaita Valley, where for now there are no standing populations of red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). In addition, the various types of damage

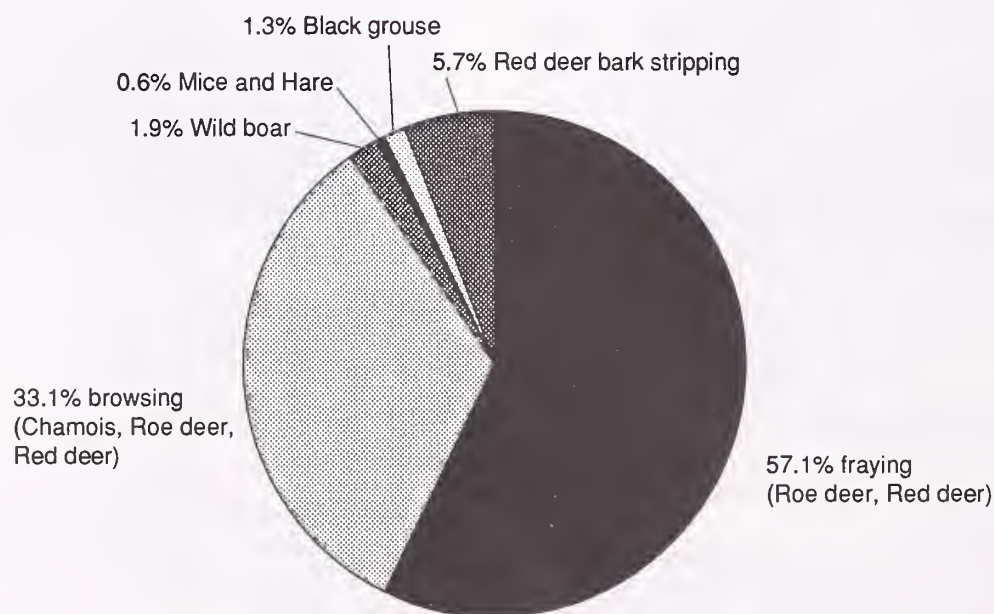


Figure 3—Wildlife damaging cembran pines in the Upper Susa Valley.

do not have the same effect, and trees are killed mainly by fraying damage caused by deer. Overall, cembran pine mortality is due primarily to damage caused by animal behavior (fig. 4).

In the areas examined, cembran pine is affected only to a limited extent by browsing because the ungulates prefer other more palatable species at lower altitudes. With respect to tree height and animal browsing, cembran pine is protected by snow in the winter months. On the other hand, saplings in the height range susceptible to fraying damage are particularly affected. A recent study (Motta and Quaglino 1989) has shown a significant incidence of fraying damage in the cembran pine compared to other species in the Upper Susa Valley. To explain this situation, we can make a number of hypotheses: a greater presence of the cembran pine in areas where this kind of damage is more likely to occur; the fact that the cembran pine remains for a considerable length of time (at least 60-80 years) within a size range prone to fraying damage; the elasticity of the young trunks to the rubbing action of the antlers; the abundance of intensely scented resin.

In the Varaita Valley, wild boars (*Sus scrofa*), which usually are favorable to forest regeneration, cause the death of a large number of cembran pine seedlings by "plowing up" the soil.

The ratio of dead to damaged trees due to wild ungulates is limited, amounting to 25.7 percent of damaged

cembran pine regeneration in the Susa Valley, 12.8 percent in the Chisone Valley, and less than 1 percent in the Varaita Valley. However, locally, for example, in the areas of red deer rut, this damage can be serious (over 65 percent of trees damaged and a 25 percent death), covering several hectares.

DISCUSSION

The spontaneous diffusion of cembran pine in the Alps of Piedmont is a phenomenon related to modifications caused by humans in the past and to the present decrease of human impact.

This phenomenon could be favored by two other factors:

- Climatic change during the last few decades (Graumlich 1991; Hansen-Bristow 1986);
- Modifications of certain parameters (numbers, density, range, etc.) and seed dispersal by the nutcracker affecting this diffusion positively.

The regeneration of cembran pine constitutes an asset from the silvicultural standpoint in that it contributes to the renewal of the topsoils that were degraded due to intense forest use by humans. For example, larch stands used for grazing are not likely to experience natural regeneration, and artificial regeneration would be somewhat problematic and very expensive. This process thus

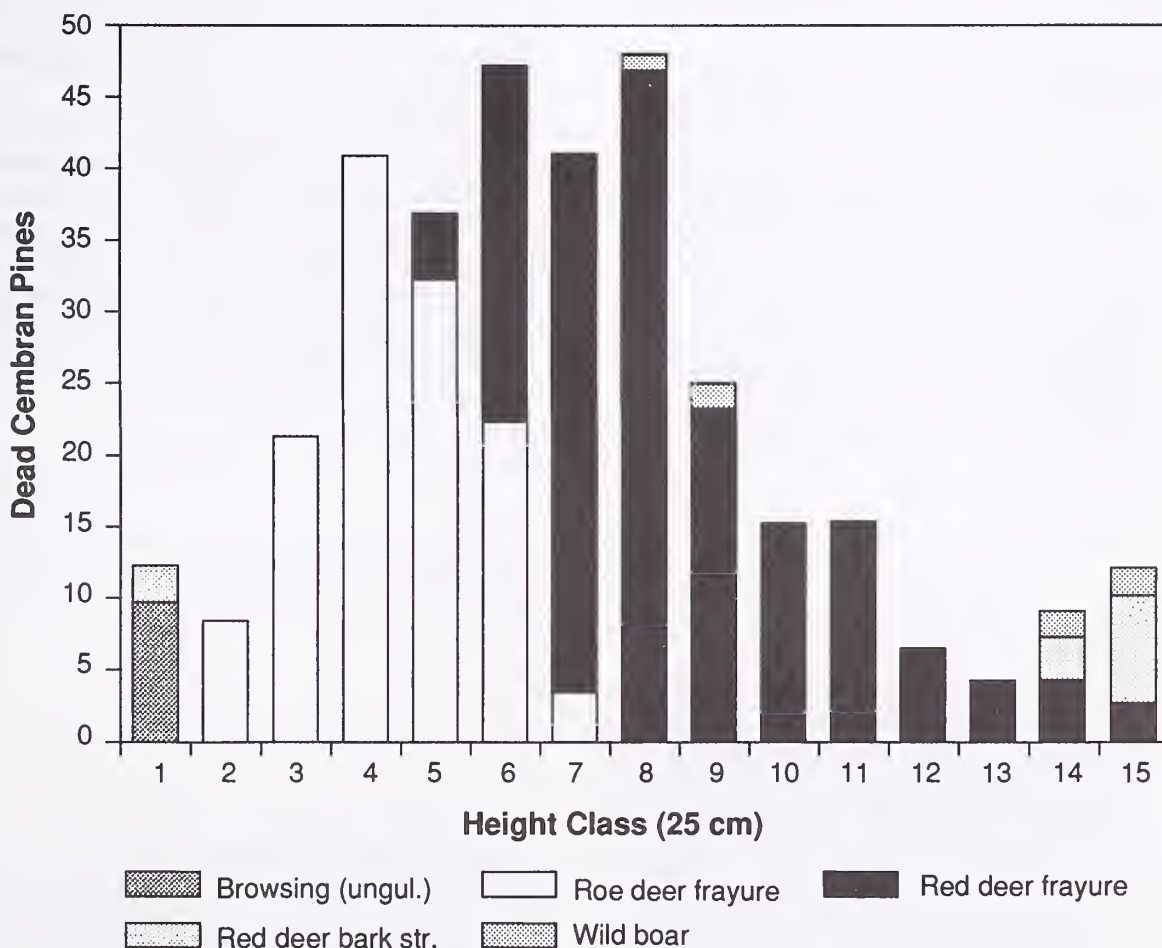


Figure 4—Cembra pine mortality caused by wildlife.

increases the physical and ecological stability of the mountain forests and enhances their protective and naturalistic value.

However, vegetation succession over very long time intervals must be taken into consideration. This is clearly evidenced by the very slow early height growth of young cembra pine. It would require but a few springs with heavy and prolonged snowfalls scattered over a range of several dozen years to favor the spread of pests such as snow fungi, and thus jeopardize the dynamic rehabilitation process that has taken decades to accomplish. However, such abundant and prolonged snowfalls occur very rarely in the valleys that have been the subject of our study, but for this very reason they constitute an even greater hazard. Thus we consider it indispensable to proceed with the monitoring of these topsoils to keep the current factors of mortality below a tolerable level and to favor, wherever possible, the formation of topsoils that are not uniform either structurally or compositionally.

REFERENCES

- Beguín, C.; Theurillat, J. P. 1982. La forêt termophile d'arolles. *Candollea*. 37: 349-379.
- Bertolani Marchetti, D. 1961. Ricerche sulla vegetazione in Valsesia. 5) *Pinus cembra* L. in Valsesia (Vercelli and Piemonte). *Nuovo Giornale Botanico Italiano*. 68(3-4): 1-3.
- Bono, G.; Barbero, M. 1971. A propos des cembraies des Alpes cotiennes italiennes, maritimes et ligures. *Allionia*. 17: 97-120.
- Contini, L.; Lavarello, Y. 1982. Le pin cembro (*Pinus cembra* L.): végétation, écologie, sylviculture et production. Paris: INRA. 197 p.
- Falcini, L. 1989. I boschi delle valli ossolane. Torino: Assessorato Agricoltura e foreste Regione Piemonte. 40 p.
- Filipello, S.; Sartori, F.; Vittadini, M. 1976. Le associazioni del Cembro nel versante meridionale dell'arco alpino (introduzione e caratteri floristici). *Atti Ist. Bot. Lab. Critt. Univ. Pavia*: 21-104.
- Giordano, A.; Mondino, G. P.; Palenzona, M.; Rota, L.; Salandin, R. 1974. Ecologia ed utilizzazioni prevedibili della valle di Susa. *Ann. Ist. Sper. Arezzo*. 5: 82-196.
- Graumlich, L. J. 1991. Subalpine tree growth, climate and increasing CO₂: an assessment of recent growth trends. *Ecology*. 72(1): 1-11.
- Hansen-Bristow, K. 1986. Influence of increasing elevation on growth characteristics at timberline. *Canadian Journal of Botany*. 64(11): 2517-2523.
- Hoffman, A. 1970. L'areale italiano del pino cembro. *Webbia*. 25(1): 199-218.
- Mattes, H. 1982. Die Lebensgemeinschaft von Tannenhäner und Arve. Eidgenössische Anstalt für das forstliche Versuchswesen. 241. 74 p.
- Motta, R.; Quaglino, A. 1989. Sui danni provocati dalla fauna selvatica ai popolamenti forestali in Alta Valle di Susa. *L'Italia Forestale e Montana*. 44(4): 241-260.
- Motta, R.; Dotta, A. 1992. Le dynamisme des mélezeins des Hautes Vallées de Suse et du Chisone (Piémont, Italie). Chambéry: Icalpe Integralp Final Report. [In print].
- Oswald, H. 1963. Verteilung und Zuwachs der Zirbe (*Pinus cembra* L.) der subalpinen Stufe an einem zentralalpiner Standort. *Mitt. der forst. Bundesversuchsanst. Mariabrunn*. 60: 437-500.
- Ozenda, P. 1985. La végétation de la chaîne alpine. Paris: Masson Ed. 331 p.
- Piussi, P.; Schneider, A. 1985. I limiti superiori del bosco e degli alberi in val di Vizze (prov. di Bolzano). *Ann. Acc. It. Sc. For.* 34: 121-150.
- Regione Piemonte; IPLA. 1982. I boschi e la carta forestale del Piemonte. Napoli: Guida ed. 177 p.
- Richard, L.; Tonnel, A. 1987. Contribution à l'étude des vallées internes des Alpes Occidentales (Première partie: originalité du milieu et quelques conséquences biologiques). *Documents de Cartographie Ecologique*. 30: 113-136.
- Stern, R. 1988. The consequences of human impact on tree borderlines. In: Saibitani, F., ed. Human influences on forest ecosystems development in Europe: Symposium proceedings; 1988 September 26-29; Trento. Bologna: Pitagora Ed.: 279-286.
- Tiraboschi, G. 1964. La presenza di formazioni spontanee di Pino cembro e Pino uncinato nelle vallate alpine novaresi con particolare riferimento alla zona dell'Ossola. Novara: C.C.I.A. di Novara. 52 p.
- Trepp, W. 1981. Das Besondere des Planterns im Gebirgswald. *Schweiz. Z. Forstwes.* 132(10): 823-846.
- Unterrichter, M. 1986. Il cirmolo. Note ecologiche, vivaistiche e selvicolturali. Milano: Regione Lombardia. 114 p.

MIXED CEMBRAN PINE STANDS ON THE SOUTHERN SLOPE OF THE EASTERN ALPS

Pietro Piussi

Abstract—Cembran pine (*Pinus cembra*) dominates over European larch (*Larix decidua*) and Norway spruce (*Picea abies*) in terms of species composition, basal area, and regeneration. Spruce and larch dominate lower and medium altitudes, pine the highest elevations. Due to intensive grazing and logging in the past, 72 percent of trees on upper timberline are under 100 years old; only 0.25 percent exceed 300 years. Forest limit is advancing. The state of health is good.

Botanical studies have been undertaken in woodlands near the upper timberline of the eastern Alps (Filippello and others 1980), but very little is known about the structure of the stands (Del Favero and others 1985; Piussi and Schneider 1985; Unterrichter 1986).

Traditionally, the upper timberline was intensively grazed during the summer, a practice still common today although numbers of domestic animals have decreased. The woods were logged for domestic and mining purposes, trees were ring-barked, and often, until recent times, seedlings were uprooted to create grazing land. Nowadays, winter sports, as well as high deer (*Cervus elaphus*) and chamois (*Rupicapra rupicapra*) populations in the absence of natural predators, exert a new kind of pressure on the timberline.

Over centuries, these activities have lowered the forest limit and substantially modified the structure, density, and regeneration patterns of high-altitude stands.

During the last 20 years, the Institute of Silviculture of the University of Florence has carried out a series of studies on woodland stands near the upper timberline on the southern slope of the eastern Alps, in order to determine the general characteristics of conifer stands in which cembran pine (*Pinus cembra*) is present and sometimes dominant. The studies established the position of forest limit and tree line, and provided data on woodland stand structure at high altitudes.

This paper analyzes the results of 10 of these studies in an attempt to reconstruct past dynamics, determine present conditions, and foresee future developments in this ecotone.

SITE DESCRIPTION

Research was conducted in three geographical areas in the provinces of Trento, Bolzano and Sondrio, northern Italy, (fig. 1):

- West: the Rhaetian Alps and Valtellina (valleys Viola, Solda, Furva, and Genova).
- Southeast: the Dolomites and central areas (valleys Fiemme, Badia, and Funes).
- Northeast: near the Austrian border (valleys Aurina and Vizze, Monte Croce Alta).

The climate becomes more continental going from the south and west, where beech (*Fagus sylvatica*) is common at lower altitudes and silver fir (*Abies alba*) can reach the forest limit, to the north, where high-altitude forests are formed by European larch (*Larix decidua*), cembran pine and Norway spruce (*Picea abies*). Precipitation decreases from south to north and its regime changes: there are spring and autumn maxima in the south and a summer peak in the north.

The terrain is rugged, and mountain tops surpass 3,000 m altitude.

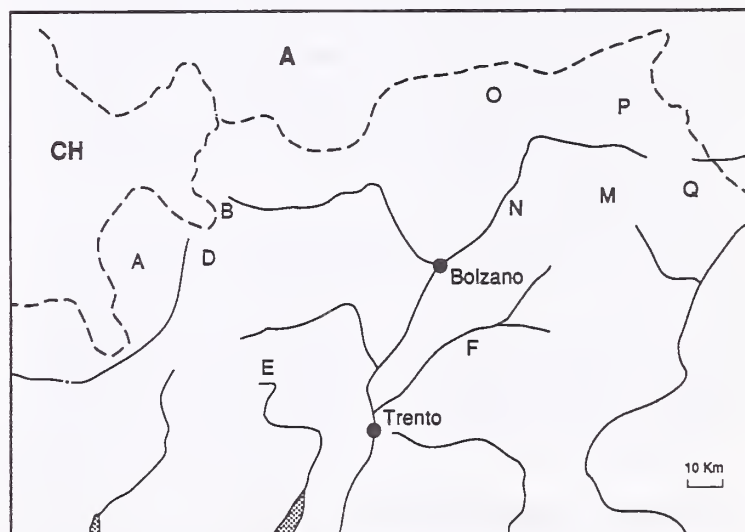


Figure 1—Study area locations and author references. A, Val Viola (Rapella 1985); B, Val di Solda (Travan 1984); D, Valfurva (Pirelli 1984); E, Val Genova (Zoanetti 1983); F, Val di Fiemme (Olivari 1983); M, Val Badia (Catalano 1987); N, Val di Funes (Maniero 1987); O, Val di Vizze (Piussi and Schneider 1985); P, Val Aurina (Hellweger 1989); Q, Monte Croce Alta (Piussi and Proietti 1986).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Pietro Piussi is Professor of Silviculture, Istituto di Selvicoltura, Università degli Studi di Firenze, Via S. Bonaventura, 13, 50145 FIRENZE, Italy.

METHODS

For every site, three determinations were made: (1) forest limit—the upper limit of woodland above 500 m² with sufficient density to create a certain woodland climate inside (Rubner, in Mayer and Ott 1991); (2) tree line for each species—the line of isolated trees above 2 m tall, as these emerge from average snow cover (Ellenberg, in Mayer and Ott 1991); and, (3) krummholz limit—individuals of tree species above the forest limit, of contorted growth and below 2 m tall due to environmental factors (Mayer and Ott 1991).

Stand conditions were examined in regularly spaced 500-m² sample plots of varying aspect and altitude, with the highest plots some 30 to 100 m below the forest limit (average 1.5 ha sampled per site; total sample area 15.4 ha). In each plot, some recordings were done for all individuals above 1.3 m height (species, d.b.h., height class, health condition) and others for a percentage of them (height, age), and for all regeneration of 0.2 to 1.3 m height (species, height class, health condition).

RESULTS

As the research evolved over a period of 2 decades, perspectives changed and some surveys carried out additional work. It has frequently been possible to separate portions of the same study area into sunny and shaded aspects and into different altitudinal bands. Data refer to individuals above 1.3 m height unless otherwise stated.

Although structure was analyzed in detail at a local scale, this paper describes only the general situation.

Forest Limit and Tree Line

Average forest limits for each study area range from 2,080 to 2,325 m above sea level (a.s.l.) (2,380 m maximum), with considerable local variation in each area. Cembran pine reaches the highest elevations, with its tree line on average 120 m above the forest limit (larch tree line 60 m, and spruce tree line 30 m above forest limit or absent).

On sites with different aspects, both forest limit and cembran pine tree line are generally higher on sunny slopes, by 20 to 30 m and about 45 m, respectively. These values are clearly lower than those given by Schroeter (1908) and Mayer and Ott (1991), who emphasize 100 m and more difference between forest limits on warm and cold slopes.

Species Composition

Cembran pine forms mixed stands with spruce and larch; rowan (*Sorbus aucuparia*) and Scots pine (*Pinus sylvestris*) are sporadic. The behavior of larch and spruce will be considered here in as much as it affects the proportion and spatial distribution of cembran pine (table 1). The relative percentage of each species depends upon site aspect and altitude.

In the west, cembran pine, dominant nearly everywhere, prefers warm slopes in Solda/Furva, whereas

Table 1—Species composition on sunny and shaded slopes

Location	Sunny slope			Shaded slope		
	Pine	Spruce	Larch	Pine	Spruce	Larch
	-----Percent-----					
Viola	50	14	36	52	16	32
Solda	82	13	5	51	2	47
Furva	87	8	5	34	—	66
Genova	—	32	68	—	11	89
Fiemme	47	49	4	70	27	3
Badia	—	—	—	35	18	47
Funes	80	15	5	71	10	19
Vizze	54	14	32	—	—	—
Aurina	83	7	10	—	—	—
Croce	15	49	36	79	21	—

in Viola aspect does not affect species composition. Larch is the second most important species.

In the southeast, in Fiemme, cembran pine is codominant with spruce on sunny sites, but leads on shaded ones, with 70 percent. In Funes, cembran pine dominance is even more pronounced, both on warm and cold slopes. Again, larch increases its presence on cold slopes, while spruce numbers decrease. By contrast, in Badia, nearly half the population on shaded sites consists of larch, with pine making up only 35 percent. There are no data for sunny slopes.

In the northeast, cembran pine dominates the south-exposed slopes of Vizze and Aurina (54 percent and 83 percent), whereas in Croce Alta cembran pine constitutes 15 percent on the sunny and 79 percent on the shaded slopes.

Average values can, however, obscure significant altitudinal variations, as is the case for Badia, Aurina, and Croce Alta, for which data divided into distinct altitudinal belts are available.

In Badia, the proportion of cembran pine increases slowly from 30 percent to 39 percent at altitudes of 1,900 to 2,100 m. In fact, the lower belt is dominated by spruce, the other two by larch. In the Aurina plots, along four belts at 1,870 to 2,340 m, cembran pine numbers increase irregularly with altitude: from 71 percent, through 86 percent and 76 percent, to 100 percent. Only on the sunny side of Croce Alta, cembran pine decreases considerably with altitude: from 22 percent in the larch-spruce dominated stand at 1,900 m to 9 percent in the spruce stand at 2,000 m. In the higher, shaded belts, cembran pine dominates spruce at 2,100 m and forms a pure stand at 2,200 m. It must be emphasized, however, that those on sunny side plots are distinctly lower than those on shaded sides.

Plant Density and Basal Area

In every study area, total plant density (number of plants per hectare) is substantially higher on sunny than on shaded slopes (table 2), varying between 800 and 900 individuals per hectare on warm and 500 and 600 individuals per hectare on cold sites. However, average values

Table 2—Plant density (number of plants per hectare) and basal area (m² per hectare)

Location	Sunny slope								Shaded slope							
	Total		Pine		Spruce		Larch		Total		Pine		Spruce		Larch	
	No.	BA	No.	BA	No.	BA	No.	BA	No.	BA	No.	BA	No.	BA	No.	BA
Viola	909	18	455	6	130	3	324	9	685	35	353	15	113	8	219	12
Solda	792	36	651	28	99	4	42	4	460	30	236	15	9	1	215	14
Furva	1,265	30	1,102	26	95	2	68	2	802	16	274	8	—	—	528	8
Genova	454	25	—	—	144	6	310	19	386	19	—	—	40	2	346	17
Fiemme	893	60	421	32	437	24	35	4	534	38	378	29	141	8	15	1
Badia	—	—	—	—	—	—	—	—	439	26	153	10	82	4	204	12
Funes	758	29	608	21	117	6	33	2	594	35	404	22	67	4	123	9
Vizze	406	23	219	13	56	2	131	8	—	—	—	—	—	—	—	—
Aurina	1,174	47	1,050	21	61	3	63	3	—	—	—	—	—	—	—	—
CroceAlta	795	37	105	5	419	17	271	15	272	23	187	21	85	2	—	—

conceal considerable site variations: in different valleys of equal aspect in the same geographical region, plant density may vary by a factor of three.

As far as individual species are concerned, the highest concentration of cembran pine is found in the western region, with 736 trees per hectare (excluding Genova where pine is absent). This average is, however, influenced by an unusually high number of pines in Furva (1,102 individuals per hectare), without which cembran pine density would have been closer to the 515 individuals per hectare recorded in the southeast.

Larch dominates the shaded slopes in the west (327 individuals per hectare), but is less important in the southeast (114 individuals per hectare).

The sunny slopes of the northeastern sites present such a great variation in tree density that averages are meaningless; and shaded slopes were monitored in one area only.

Average basal area (table 2) revolves around 30 m²/ha, being only a little higher on sunny slopes. Values show a narrower range than those of tree numbers per hectare, indicating an efficient use of available land.

Diameter Distribution

As shown in figure 2, the number of individuals generally decreases, even if irregularly, with increasing diameter class; and the distributions are continuous to about 65 cm d.b.h., with an occasional scatter of trees in size classes 85 to 110 cm.

In most cases, the majority of cembran pine, larch, and spruce are contained in the size classes up to 30 cm: (for example, Solda, warm slope: 80, 50, and 75 percent; Badia, cold slope: 65, 60, and 82 percent) and, quite frequently, concentrated solely in the smallest d.b.h. class, to 10 cm (for example, Viola, warm slope: 81, 59, and 49 percent; Furva, warm slope: 53, 64, and 75 percent).

At some sites, the shape of the distribution shows a "hump" at the 30 to 50 cm d.b.h. class level: as on the cold slopes of Viola, Genova, and Badia; in Fiemme; and on the warm slope of Croce Alta. This affects larch and spruce to a greater extent than cembran pine.

Bigger size classes contain more spruce and larch than cembran pine, with the exception of some large pines on north-facing slopes.

Looking at the d.b.h. distribution in relation to altitude, in Badia the percentage of small-diameter larches rises with increasing altitude; likewise, the number of big cembran pine trees increases and that of large spruces and larches diminishes. In Aurina, the number of small cembran pines increases with altitude, with spruce and larch disappearing altogether in the highest belt.

Age Structure

Since age structure was analyzed only in some of the study areas, and results were not given for each species separately, figure 3 shows the "cored ages" of all trees, in 25-year classes, to which must be added the time taken to reach 1.3 m height.

Cembran pine, spruce, and larch in Viola take on average 15, 30, and 40 years; cembran pine in Furva 20 and in Funes 30 years to grow to 1.3 m, which explains the apparent lack of trees up to 25 years old and the reduced percentage of 26- to 50-year-olds.

But even so, the histograms show young populations: in Viola (and Furva), 79 percent (86 percent) of the trees are younger than 100 years and only 7 percent (6 percent) are older than 150 years. In Viola, the oldest trees found were 281 (larch), 274 (spruce), and 150 (pine) years old, whereas in Furva the oldest cored tree is a cembran pine of 310 years; the oldest larch and spruce are 244 and 230 years old.

In Funes, 49 percent of trees are under 100 years old, but all age classes to 300 years are well represented. The oldest 1 percent of trees are in the 326 to 450 age classes, including a larch, a cembran pine, and a spruce at 431, 396, and 289 years old.

In Aurina, tree populations become progressively younger with altitude. Rising from the lowest to the highest belt, the proportion of trees under 100 years old is 57, 74, 62, and 91 percent. Belt 3, at nearly 2,200 m a.s.l., contains the oldest trees, with 17 and 5 percent, respectively, in the 201 to 250 and 251 to 300 age classes.

The oldest trees stem-cored were at Vizze: a 557-year-old larch and a cembran pine of 443 years.

A proportional relationship between age and diameter exists only within very wide margins so that tree sizes do not allow age estimates; thus, a 25 cm d.b.h. Vizze pine

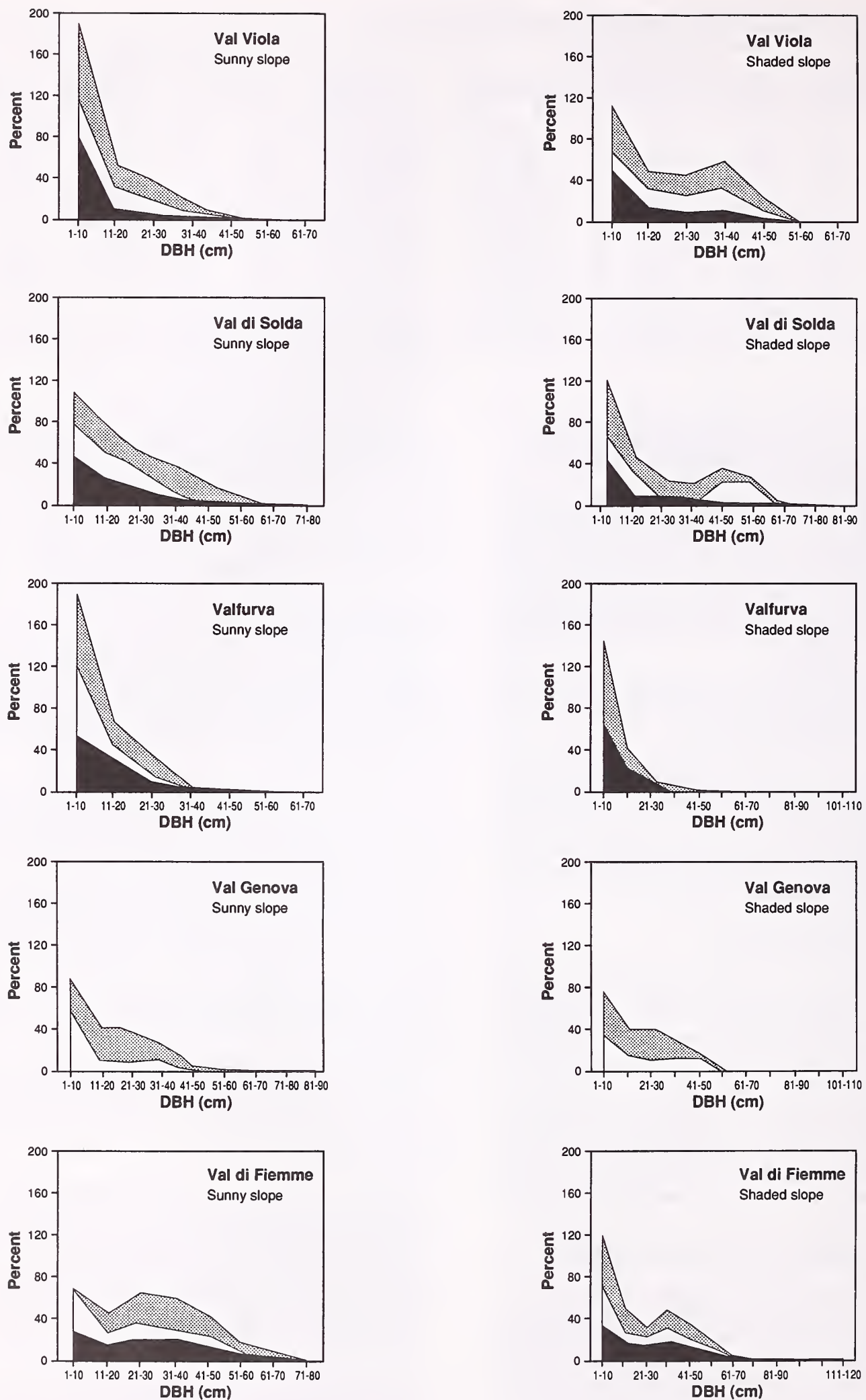


Figure 2—Diameter distribution of pine, spruce, and larch.

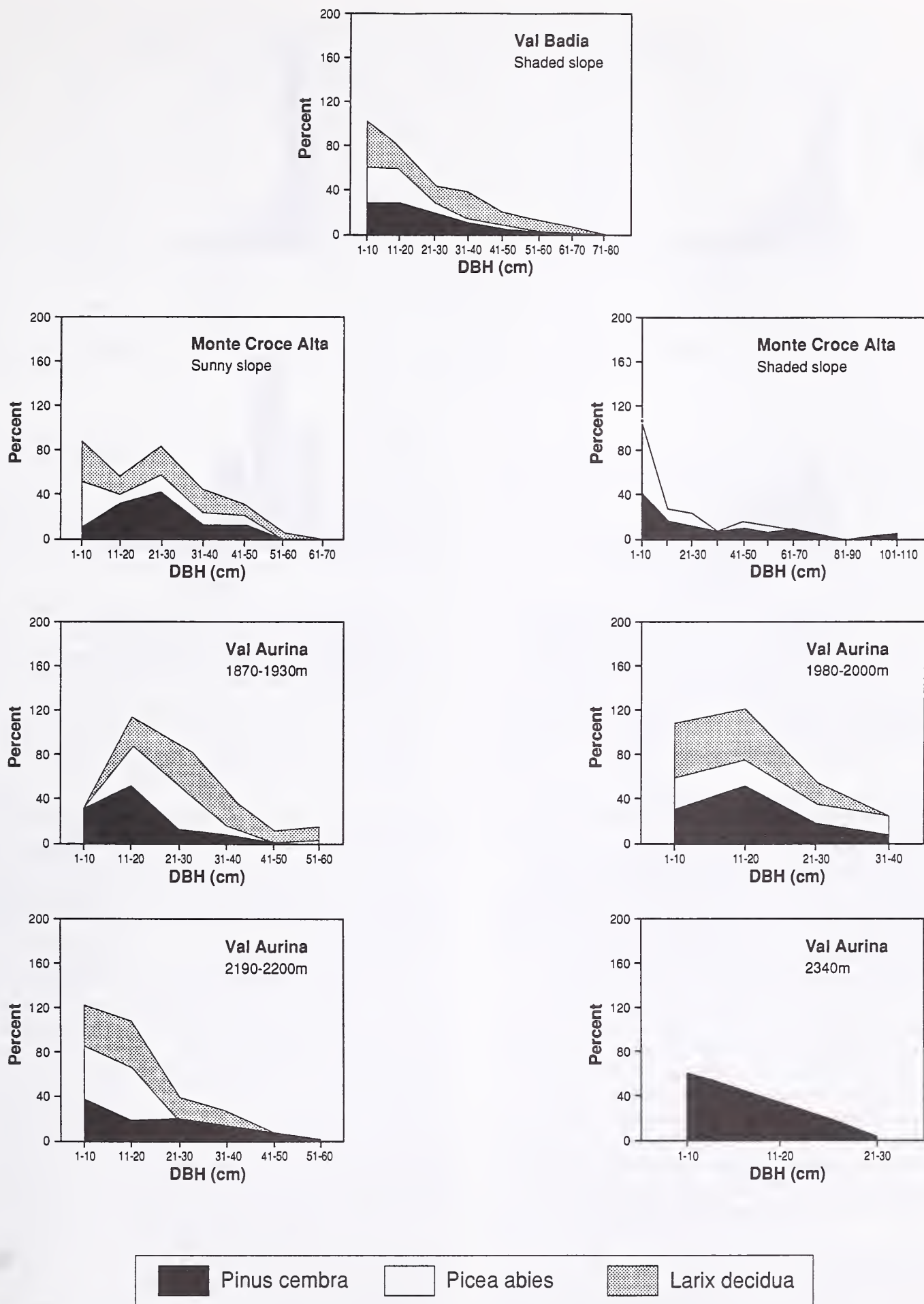


Figure 2 (Con.)

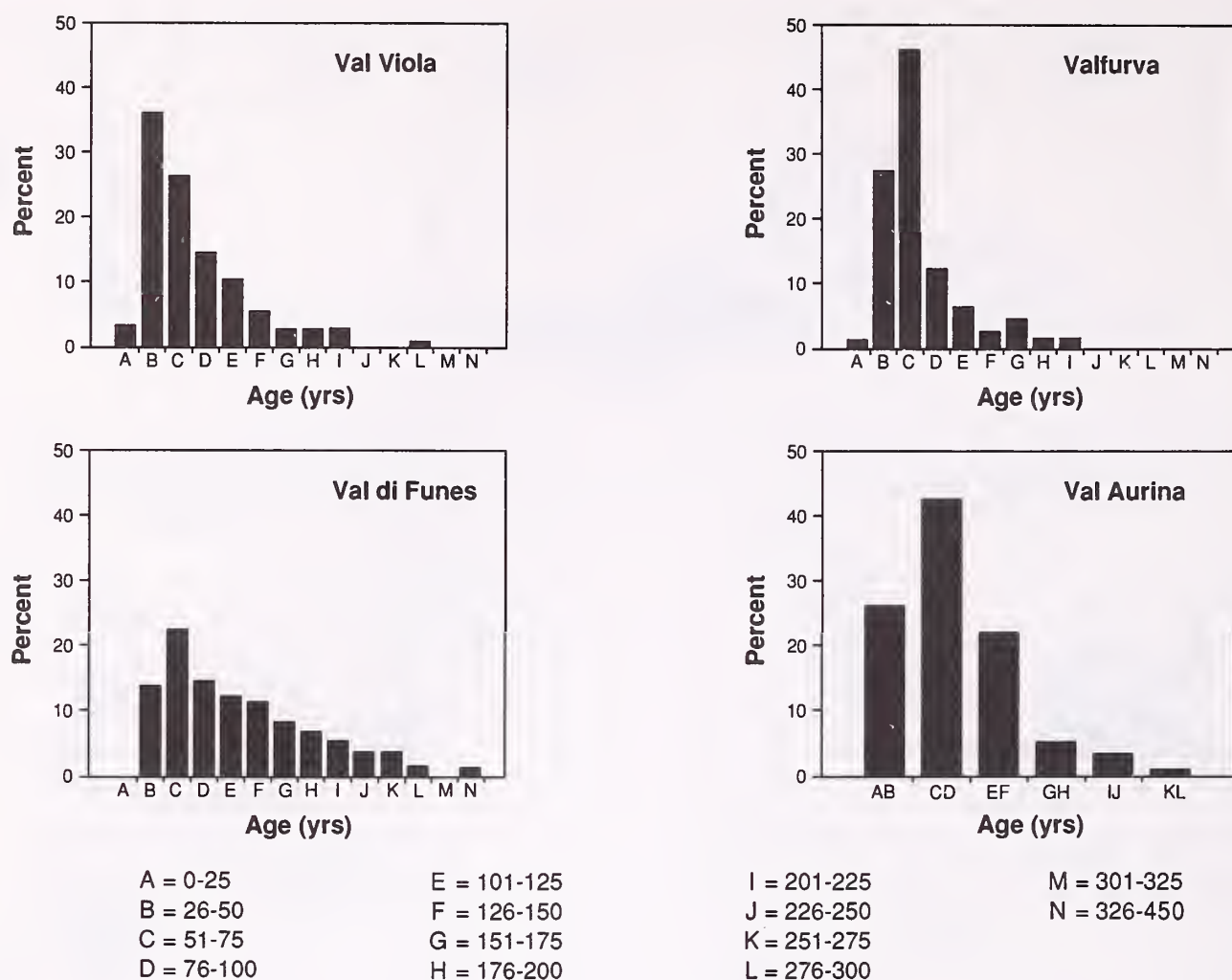


Figure 3—Age distribution of pine, spruce, and larch.

can be from 60 to 250 years old, and at 100 years of age its d.b.h. may range from 10 to 50 cm.

From the d.b.h. distribution, the "cored age" range per species for each 10-cm d.b.h. class and the approximate age of trees at 1.3 m "cored" height, stand development on the shaded Viola slope was cautiously reconstructed. The oldest larch and spruce found date from the 1660's and 1680's, the oldest cembran pines only from the 1820's. The 1750's-1820's saw ample larch recruitment parallel with a spruce maximum from the 1780's-1850's, still testified to by today's peak in the 30- and 40-cm d.b.h. classes. Larch recruitment culminated in the 1830's-1930's when 40 percent of today's population (to 10 cm d.b.h.) was established; now regeneration is continuing at a slower pace. Cembran pine recruitment accelerated after the 1850's. Indeed, 51 percent of today's population (to 10 cm d.b.h.) dates from 1870-1970 and regeneration continues strongly, while spruce regeneration is being reduced.

Regeneration

Table 3 shows that plant density varies considerably between study areas (from 111 to 1,646 individuals per hectare at Genova and Viola); in fact, area averages conceal

notable variations between plots. Also, plant density is usually higher on sunny than on shaded sites.

Nearly everywhere, cembran pine regeneration prevails over that of spruce and larch by a large margin, more so on warm than on cold slopes. Spruce definitely prefers warm sites.

To detect another indicator of stand dynamics, a comparison was made between the species composition of the adult stand (table 1) and that of regeneration. As a general trend, the dominance of cembran pine in the adult stand is being consolidated by an even higher proportion of regeneration. This happens in Viola, on the cold slopes of Solda, Fiemme, and Croce Alta, in Vizze and Aurina, and on the sunny slope of Funes. The larch wood with cembran pine on the shaded side of Furva experiences increased cembran pine regeneration, and the sunny spruce-pine stand of Fiemme now contains more than twice as many small cembran pines as spruces.

An enquiry dealing with regeneration in the western region (Bettini 1987) showed that at lower altitudes (1,700 to 1,800 m) cembran pine establishes mainly in large clearings within the wood. It does best, in terms of density, at higher altitudes (1,900 to 2,200 m) where it preferably occupies large clearings, open spaces just outside the woods, and open, multistoried woods.

Table 3—Regeneration: plant density (individuals per hectare) and species composition of plants ≥ 0.2 m <1.3 m height

Location	Sunny slope				Shaded slope			
	Total	Pine	Spruce	Larch	Total	Pine	Spruce	Larch
	No.	-----Percent-----			No.	-----Percent-----		
Viola	1,646	70	9	21	745	61	7	32
Solda	207	74	13	13	400	68	1	31
Furva	673	87	8	5	518	43	0	57
Genova	111	0	38	62	128	0	20	80
Fiemme	303	67	30	3	277	89	10	1
Badia	—	—	—	—	312	37	26	37
Funes	412	87	8	5	207	64	3	33
Vizze	849	80	4	16	—	—	—	—
Aurina	458	88	4	8	—	—	—	—
Croce	1,249	25	24	51	459	84	6	10

Health Conditions

According to a visual examination of the trees, the state of health of the timberline woods is good. On average, 75 percent of individuals were considered healthy; 14 percent suffering; 3 percent dying; and 4/4 percent standing/lying dead.

The majority of dead and dying individuals are small trees, with diameters to 15 cm (Genova) or 30 cm (Fiemme), whereas the proportion of mortality involving big trees (above 55 cm d.b.h.) varies, being virtually nil in Fiemme and 30 percent of deaths in Vizze.

Generally, deaths of young plants are due to competition, trampling, browsing, and snow fungi; mortalities of larger trees are caused by lightning, avalanches, and landslides.

DISCUSSION

The stand structure of mixed cembran pine, European larch, and Norway spruce woodlands at the upper timberline is extremely diverse on a local scale. Timberline limits, species composition, plant density, regeneration, diameter distribution, and age structure vary between adjacent sites of the same valley studied, from one study area to another, between sunny and shaded slopes of the same valley, and between different altitudes, apparently as a result both of physical environmental factors and of human action, frequently hard to detect and explain.

The sequence of altitudinal limits (forest limit being succeeded by spruce tree line, followed by larch tree line, topped by cembran pine tree line) is somewhat higher on sunny slopes than on shaded ones, probably due to more favorable site conditions such as extended insolation, higher temperatures, and earlier snow melt.

In fact, spruce distribution seems to be strongly limited by heat deficiency. Larch is usually more numerous on cold sites and is well represented at all altitudes except for the highest locations. At a first glance, cembran pine appears to have no preference as to aspect. However, its performance is closely linked to the behavior of spruce

and larch, as cembran pine is dominating where the latter two species show constraints. Virtually everywhere, therefore, cembran pine dominance increases with altitude.

The timberline woods are predominantly young stands in various phases of development: 72 percent of the trees are younger than 100 years; 23 percent belong to the 101 to 200 year class; 4.75 percent to the 201 to 300 year class, and 0.25 percent are over 300 years old.

This age structure reflects centuries of unabated exploitation, which culminated in the last century, and the subsequent progressive abandonment of the mountains with the decline of agriculture, which has given rise to the spontaneous recolonization of derelict pastures and degraded woodlands.

As the more inhospitable, shaded slopes were abandoned first, woodland returned there earlier, as shown by a larger proportion of medium-sized trees on cold slopes.

The fact that bigger d.b.h. classes contain more spruce and larch than pine, except on some cold slopes, clearly reflects the traditional practice of eradicating cembran pine, which shaded the pasture. Since this intervention ceased, cembran pine has been able to reclaim especially those areas with reduced competition from the other two species: aspects and altitudes too cold for spruce, and woodland stands too dense for larch regeneration. As a result, cembran pine now dominates the young generation at virtually all sites and continues to colonize high altitudes.

However, tree vegetation is favored on sunny aspects: benefiting from a more favorable microclimate and greatly reduced disturbance, there is higher tree density and more regeneration than on shaded slopes.

And changes are still under way at timberline: density is increasing, cembran pine percentage is rising, woodland area is expanding to higher elevations.

It is assumed that the present forest limit is lower than the potential one. It is not clear whether all the area between forest limit and tree line can be occupied by the new stands, whose edges are sometimes abrupt, but the irregular ecotone formed by scattered trees seems to be the result either of difficult edaphic conditions or of human activity and cannot be considered an expression of climatic conditions.

REFERENCES

- Bettini, D. 1987. La rinnovazione naturale in un bosco di *Picea*, cembro e larice nella Valle del Torrente Frodolfo (prov. di Sondrio). University of Firenze. 109 p. Thesis.
- Catalano, L. 1987. Studio del limite del bosco nei complessi di Stores e Settsass nell'alto bacino del fiume Gadera (prov. BZ e BL). University of Firenze. 152 p. Thesis.
- Favero del, R.; Mas de, G.; Lasen, C.; Paiero, P. 1985. Il pino cembro nel Veneto. Regione del Veneto. 85 p.
- Filipello, S.; Sartori, F.; Vittadini, M. 1980. Le associazioni del Cembro nel versante meridionale dell'arco alpino, 2. La vegetazione: aspetti forestali. Atti dell'Istituto Botanico e Laboratorio Crittogamico dell'Universita' di Padova. 14: 1-48.
- Hellweger, V. 1989. Il limite superiore del bosco e degli alberi e le condizioni del bosco di alta montagna a Riva di Tures in Val Aurina (BZ). University of Firenze. 170 p. Thesis.
- Maniero, R. 1987. Il limite superiore del bosco e degli alberi in Val di Funes (BZ). University of Firenze. 127 p. Thesis.
- Mayer, H.; Ott, E. 1991. Gebirgswaldbau Schutzwaldpflege. Stuttgart: Gustav Fischer Verlag. 587 p.
- Olivari, M. 1983. Il limite superiore del bosco e degli alberi in alcune zone della Val di Fiemme (TN). University of Firenze. 70 p. Thesis.
- Pirelli, P. 1984. Composizione e struttura del bosco in alta montagna in Val dei Forni, Valfurva e Val Zebbru'. University of Firenze. 72 p. Thesis.
- Piussi, P.; Schneider, A. 1985. I limiti superiori del bosco e degli alberi in Val di Vizze. Annali dell'Accademia Italiana di Scienze Forestali. 34: 121-150.
- Piussi, P.; Proietti, A. M. 1986. Struttura e rinnovazione del pino cembro a Monte Croce Alta. Unpublished manuscript. 22 p.
- Rapella, A. 1985. Il limite superiore del bosco e degli alberi in Val Viola (SO). University of Firenze. 116 p. Thesis.
- Schiechtl, H. M.; Stern, R. 1975. Die Zirbe (*Pinus cembra* L.) in den Ostalpen, I. Teil. Angewandte Pflanzensoziologie. 23: 1-84.
- Schroeter, C. 1908. Das Pflanzenleben der Alpen. Zuerich: Albert Raustein Verlag. 806 p.
- Travan, L. 1984. Struttura e rinnovazione nei boschi in alta montagna in Val di Solda. Unpublished manuscript. 37 p.
- Unterrichter, M. 1986. Il Cirmolo. Note ecologiche, vivaistiche e selvicolturali. Regione Lombardia. 84 p.
- Zoanetti, R. 1983. Il limite superiore del bosco e degli alberi in Val Genova (Trento). University of Firenze. 73 p. Thesis.

CURRENT DISTRIBUTION OF CEMBRA PINE IN THE LECHTAL ALPS

Siegfried Sauermoser

Abstract—The Lechtal Alps are located at the northern rim of the Alps. In these mountains the subalpine forests are dominated by spruce (*Picea abies*) and by mountain pine (*Pinus mugo*), while only a few cembra pine (*Pinus cembra*) stands are found there. Cembra pine occurs in 15 different places, each of them more than 5 hectares.

In Austria, we have the so-called forest-technical service system for torrent and avalanche control, which means that we are not only responsible for regular hydraulic engineering and technical measures, but also for reforestation of torrent catchments or avalanche areas, for example, and for the maintenance and establishment of the protective forests in our Country. The forest-technical system of torrent and avalanche control originated in France and was introduced to Austria during the middle of the last century.

The forest-technical service has replanted about 2,500 hectares of timberline area during the last 30 years, mainly using spruce (*Picea abies*), larch (*Larix decidua*), and cembra pine (*Pinus cembra*).

Cembra pine is an especially important tree for afforestation in protective forests. Being an evergreen conifer, it possesses the highest snow interception (Aulitzky 1982), which is extremely important for reforestation in avalanche areas. In addition, cembra pine is very long-lived and is able to form stable forest stands (Mayer 1977). Moreover, it is the most frost-resistant subalpine tree (Tranquillini 1963).

Cembra pine grows well on crystalline substratum in the central alpine area, where it is primarily used. The situation is quite different at the northern rim of the limestone mountains. Cembra pine is not as common there, and reforestation with cembra pine must be more carefully related to site conditions than in the central Alps. In the limestone Alps cembra pine occurs only in a very small area and is not important to the forestry industry. Thus, there are only a few studies on it, although cembra pine is very important for the protective forests. The only study about silvicultural treatment and natural regeneration in a cembra pine-larch forest of the northern limestone mountains was done by Kleine (1984).

The following questions would be of special interest to the expert:

- How do the present cembra pine stands develop, how old are they, what are their degree of stability and the potential for regeneration?
- How do these cembra pine stands develop under the influence of the decline of grazing, on the one hand, and the high game population on the other?
- How much was the distribution of cembra pine influenced by human activities, and what was the original distribution?
- And the most important question: on which sites can cembra pine be successfully used for reforestation?

However, due to the fact that our research did not begin until last year, I cannot answer these questions yet; but I will try to give you a survey of the present cembra pine stands in the Lechtal Alps.

LOCATION

The Lechtal Alps are located at the northern rim of the limestone Alps between the 10th and 11th longitudinal degree (east of Greenwich) and between the 47th and 48th latitudinal degree (fig. 1). From east to west they extend for about 60 kilometers and for about 20 kilometers in the north-south direction. The total area is about 1,000 km².

CLIMATE

The location on the northern border of the Alps results in a high precipitation level in summer as well as in winter. The average precipitation level along the Lechtal is

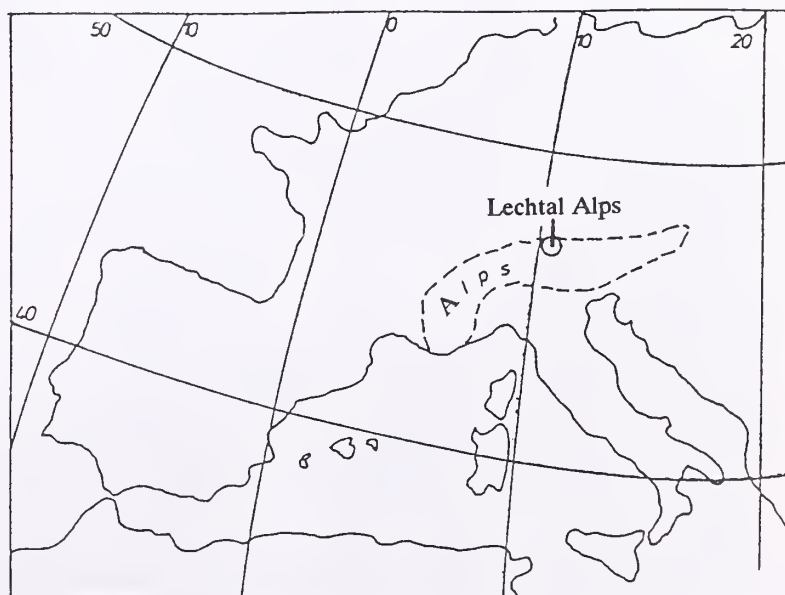


Figure 1—Lechtal Alps location.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Siegfried Sauermoser is Engineer of the Technical Forest Service for Torrent and Avalanche Control, 6600 Lechaschau, Austria.

between 1,200 mm and 1,400 mm per year at an elevation of 1,000 m. Air currents from the west and northwest bring moist air from the Atlantic regions, and, when forced crossing the mountains, frequent rain falls in this area.

From the climatological point of view, the position of plant communities can be described by the angle resulting from the local amount of precipitation drawn versus elevation of the area. Areas that would be located in the sector >45 degrees are considered to have a continental climate (= "hygrische Kontinentalität," Gams 1931). The "hygrische Kontinentalität" of the Lechtal Alps lies between 40 and 50 degrees (fig. 2). The central-alpine regions, main area of larch-cembra pine forests, are more continental (70-90 degrees).

GEOLOGY

Geologically, the Lechtal Alps are very complicated. The landscape is primarily determined by two mountain ranges. The main mountain range is dolomite, which forms rugged, sterile mountains. In these dolomite areas, the most common soil is redsina, with differing depths of humus layer. The southern slopes are particularly gentle and dry, due to easy infiltration of precipitation water.

On the other hand, there are mountains that are composed of marl, that is more susceptible to weathering and erosion. These areas, characterized by a more smooth topography, are covered with vegetation up to the mountain tops. The soil is deeper, compared to the dolomite mountains, and rich in clay, while the humus layer is shallower. In these mountains, the effects of anthropogenic influence are especially evident as they have been cleared and cultivated for centuries (fig. 3).

VEGETATION AND PLANT COMMUNITIES

The valleys of the Lechtal Alps are located at an elevation of about 1,000 m, and the highest peaks are 3,000 m high. Due to elevation and climatic conditions, which are strongly influenced by air currents from the Atlantic, the Lechtal Alps are characterized by typical north alpine vegetation. Spruce and spruce-fir (*Abies alba*) forests dominate up to an elevation of about 1,500 m, especially on the northern slopes.

The timberline is located at about 1,900 m, and is formed by different tree species. Mountain pine (*Pinus mugo*) prevails and forms large stands in the dry dolomite

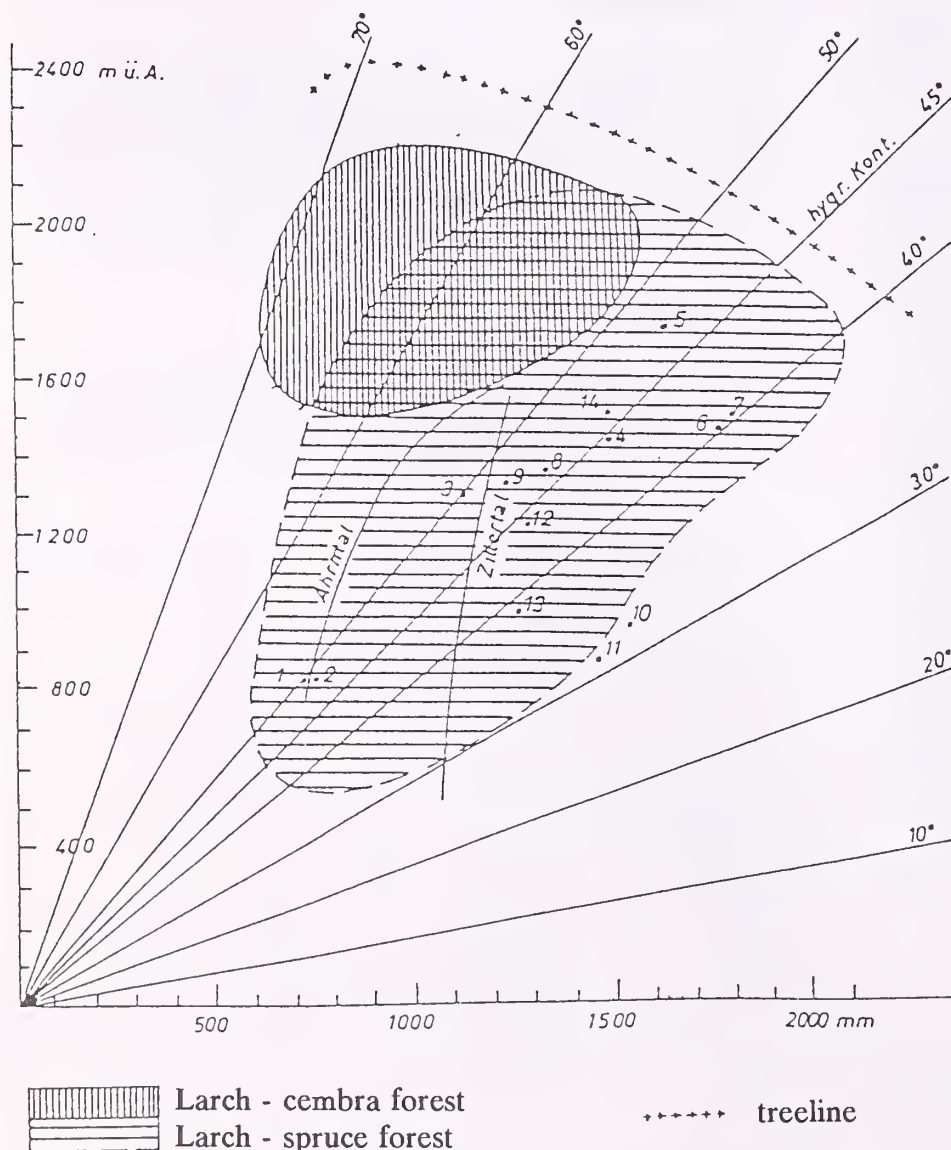


Figure 2—"Hygrische Kontinentalität" according to Gams (1931) for different forest types and geographical regions. The points 1-13 show different sites of the Lechtal Alps. The points 1, 2, and 3 are on the southern rim (more continental); the points 10 and 11 on the north rim indicate climatic conditions more influenced by air currents from the Atlantic.



Figure 3—Typical mountains composed of marl in the Lechtal Alps. The clearcut slopes have been used for agriculture since the 14th century. After the strong decline of livestock farming the slopes will be reforested to create protective forests.

areas. Spruce and fir or larch appear only singly here. This type of forest, including large stands of dwarf mountain pine with single spruce or larch trees, is found primarily on southern slopes. In marl areas, the forest limit is mostly formed by spruce. On moist northern slopes it is joined by green alder (*Alnus viridis*).

Where can cembra pine be found in the Lechtal Alps?

Cembra pine occurs in about 20 different places, each with a coverage of more than 5 ha. The largest stand of cembra pine is about 20 ha. In many other places, cembra pine occurs singly in contact with other tree species.

When comparing the distribution pattern of cembra pine with the geological map, it becomes obvious that cembra pine grows primarily on dolomite and limestone, but is less frequent on marl. There also is a relationship of cembra pine range to soil conditions as it occurs in contact areas between dolomite and marl. Haupt (1983), in his study on the forest communities of the Lechtal Alps,

also observed this phenomenon. Similar observations were made farther east in the Karwendel Mountains by Vareschi (1931). Vareschi found the occurrences of cembra pine in the upper Isar Valley to be related to layers of dolomite and raibler. Raibler stratum is a geological formation consisting of different limestones and marls.

Although mainly marl areas were cleared and settled, this cannot be the only reason for the absence of stone pine on marl. I believe germination conditions to be worse on marl than on dolomite, because of the shallow humus layer, smooth topography with long-lasting snow cover, and stronger vegetation competition on the nutrient-rich soils. If stone pine is artificially introduced to marl areas, it shows great fertility, which might support the theory that cembra pine is less frequent on marl because of its low competition ability. Moreover, as cembra pine seeds germinate most successfully at moisture conditions of 60-70 percent and temperatures between 20 and 22 °C



Figure 4—Southwest-exposed plateau, the so-called “cembra pine-flatland” with cembra pine-spruce-mountain pine forest.

(Nather 1958), marl soils might be considered to be too cold to allow successful regeneration.

The situation is different on redsina, which can occur on dolomite. Cembra pine can be found on northeast and northwest knolls and ridges, where, due to low erosion, high raw humus layers can develop. Therefore, cembra pine is primarily found on knolls and crests that are northeast or northwest exposed. There is only one larger stone pine stand on south- or southwest-exposed slopes. It is called the “cembra pine flat land” and, as the name indicates, it is a plateau at an altitude of about 1,800 m (fig. 4). The other cembra pine stands are located between 1,300 and 1,950 m.

At lower elevations, cembra pine often occurs associated with fir, mountain maple (*Acer pseudoplatanus*), or beech. These are contact areas for mixed forests, which are also found primarily on northern exposures. Cembra pine and spruce are often found together, and contact to the subalpine spruce forests is very common.

In the Lechtal Alps, larch and cembra pine are seldom found together. There is only one forest where the number of larch trees exceeds cembra pines, and where regeneration of larch is abundant. Contact with the spruce is much more common in the Lechtal Alps (fig. 5). Without pollen analysis studies, it is difficult to guess how much forest communities are anthropogenically influenced, or whether this phenomenon is simply the result of natural forest development on carbonate ground. Mayer (1974) described three varieties of “carbonate-larch-cembra pine forests” (*Larici-Cembretum-Rhododendretosum hirsuti*). He differentiated between the typical form on plateau areas, the high shrub-green alder variety occurring on lias-dogger substratum, and the mountain pine variety. The Lechtal Alps’ stone pine forests are for the most part to be attributed to the dwarf mountain pine variety. The transition to pure dwarf mountain pine forests is fluid and cannot be sharply defined.

STRUCTURE AND AGE

Cembra pine generally stands very loosely and is concentrated only in a very small area on exposed mountain ridges. At 24 sites, the maximum age of cembra pine was determined by tree-ring dating. At each site, the visually oldest tree was examined. The tree ages ranged from 150 to 600 years. The apparently oldest cembra pine dated has a diameter of 111 cm and is probably about 600 years old. An exact age determination was not possible because the trunk is rotten. Thus, the age was only estimated, referring to comparable trees. In the group containing this old cembra pine, there are four other cembra pine trees, in the middle of a stand of dwarf mountain pine. These stone pines are about 330, 290, 190, and 150 years old. These age differences in cembra pine stands, which became apparent from the increment cores, cannot be recognized with the naked eye, as the trunks look more and more the same when getting older.

REGENERATION

Regeneration is primarily found, as in the central alpine regions (Oswald 1963), on sites with early snowmelt such as small hummocks. They are usually built up by organic matter originating from moss and dwarf-shrub vegetation. The organic layer is approximately 30 to 40 cm thick. It is separated from the dolomite bedrock by a narrow weathered horizon. The sites are covered with *Pinus mugo*, *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Calamagrostis villosa*, and *Homo-gyne alpina*. The dominating mosses are *Hylocomium splendens*, *Dicranum scoparium*, *Polytrichum formosum*, *Rhytidiadelphus triquetrus*, and *Pleurozium schreberi*. On the dwarf-shrub hummocks there are acidophilic plants, while between and around the small hills there are more calcicolous plants like *Calamagrostis varia*, *Sesleria varia*, *Carex sempervirens*, *Carex firma*, *Rhododendron hirsutum*, and *Carex ferrugineum* (fig. 6).



Figure 5—Typical open cembra pine stands mixed with mountain pine.



Figure 6—Typical natural regeneration site of cembra pine and spruce on a dwarf-shrub hummock.

Apparently, the decline of alpine grazing had a positive effect on regeneration of cembra pine. Although exact studies are still needed, cembra pine regeneration occurs especially in the areas of former alpine pastures. Most of the plants are up to 30 cm high. Larger plants are rare. As previously mentioned, this could be explained by regeneration of cembra pine during the last 30 years (since the decline of grazing). However, it may also be possible that cembra pine is not able to grow higher under the present climate.

In this connection, the damage done by game to cembra pine should be mentioned. In our afforestations game does harm mainly to cembra pine. Unfortunately, in the Lechtal Alps decline of alpine grazing runs parallel with an increase in game. So today, game density is very high in this area. Only exact studies will be able to determine the degree of damage caused to the artificial and natural regeneration of cembra pine.

I hope to have given you a small survey on the cembra pine occurrences in the Lechtal Alps. However, additional information can only be expected from more exact studies in the future.

REFERENCES

Aulitzky, Herbert; Turner, Hans. 1982. Bioklimatische Grundlagen einer standortsgemäßen Bewirtschaftung

- des subalpinen Lärchen-Arvenwaldes. Mitt. Eidg. Anst. f. Forstl. Versuchswesen. 58(2). 579 p.
- Gams, Helmut. 1931. Die klimatische Begrenzung von Pflanzenarealen und die Verteilung der hygrischen Kontinentalität in den Alpen. Zeitschr. der Ges. für Erdkunde zu Berlin. 9/10: 331-346.
- Haupt, Wolfgang. 1983. Die aktuelle Vegetation der östlichen Lechtaler Alpen. I. Waldgesellschaften. Veröff. Museum Ferdinandeum Innsbruck Bd. 3. 67 p.
- Kleine, Michael. 1984. Waldbauliche Untersuchungen im Karbonat-Lärchen-Zirbenwald Warscheneck/Totes Gebirge mit Verkarstungsgefahr. Diss. Boku. 150 p.
- Mayer, Hannes. 1974. Wälder des Ostalpenraumes. Gustav Fischer Verlag, Stuttgart. 344 p.
- Mayer, Hannes. 1977. Waldbau. Gustav Fischer Verlag, Stuttgart. 483 p.
- Nather, Hans. 1958. Zur Keimung der Zirbensamen. Centralblatt ges. Forstwesen. 75: 61-70.
- Oswald, Helfried. 1963. Verteilung und Zuwachs der Zirbe (*Pinus cembra* L.) der subalpinen Stufe an einem zentralalpinen Standort. Mitt. Forstl. Bundesversuchsanstalt Mariabrunn. 60: 437-500.
- Tranquillini, Walter. 1963. Über die Frostresistenz der Zirbe. Mitt. Forstl. Bundesversuchsanstalt Mariabrunn. 60: 547-562.
- Vareschi, Volkmar. 1931. Die Gehölztypen des obersten Isartales. Universitätsverlag Wagner, Innsbruck.

GEOGRAPHICAL DIFFERENTIATION AND DYNAMICS OF SIBERIAN STONE PINE FORESTS IN EURASIA

E. P. Smolonogov

Abstract—The study reported here is based on comprehensive long-term investigations (1960-90). Regularities in geographical differentiation and biogeocenotic polymorphism of stone pine forests as well as rhythmic changes in forest composition and forest structure dependent on reproduction and age dynamics are considered. Based on these ecological aspects a system that allows control of the structural development of the coenosis (morpho-coenogenesis) and a strategy for use, restocking, and preservation of stone pine forests were developed. Stone pine forests are the most essential landscape structures of the Ural-Siberian taiga.

In Eurasia, forests that include or are dominated by Siberian stone pine extend over almost 70 longitudinal degrees from the western foothills of the Urals to the upper drainage area of the Aldan River in eastern Siberia and over 22 latitudinal degrees from north to south, from the lower Enisei River to the upper drainage area of Orkhon River. The total area covered by the stone pine forests amounts to 40 million hectares. Over 95 percent of the forest area belongs to Russia, the rest to northern Mongolia.

The formation of modern ranges of stone pines and propagation of forests with stone pines in Eurasia was influenced by multiple intermittent glaciations. It is supposed that stone pines had a continuous range before the glacial epoch, while during cold periods they survived only in some upland refugia in Europe, in the Urals, in Siberia, and in central south-eastern Asia (Kolesnikov 1956; Luzganov and Aboimov 1977; Neishtadt 1957; Nepomilueva 1974; Tolmachev 1954; and others). This might explain why Swiss and Siberian stone pines became separate species (Bobrov 1978).

A TWO-PART RANGE

B. P. Kolesnikov (1966) considers Siberian stone pine a developing species that still is extending. In fact, compared to other stone pines, it has the widest range. Siberian stone pine grows and propagates well under severe highland conditions of the Urals, southern Siberia, and central Asia, but stone pine forests also occupy large areas

on swampy fluvioglacial and alluvial plains of western Siberia. Stone pine that immigrated from the southern regions to western Siberia did not occur there before 10,000 to 20,000 years ago.

Hence, with respect to this history, the range of this species should be divided into two parts: the younger forested part of the Urals, western and eastern Siberia, where migration of the stone pine and other forest-forming species followed deglaciation, and, on the other hand, the ancient part of the mountain systems of southern Siberia and central Asia, where stone pine has been existing for many millions of years, forming stable mountain-forest flora complexes.

Also, the plains of western and eastern Siberia are not homogeneous. From north to south they are divided into latitudinal forest zones and subzones (Krylov 1961; Smolonogov and others 1970), which are different in total duration of forest-, swamp-, and soil-forming processes (from 2,500 to 3,000 to 10,000 to 12,000 years), thermal and energy conditions, and character of biosphere processes. The differences are great. The northern forests are mainly found on continuous permafrost soils, thus growing under present periglacial conditions, while the southern and middle forest zones are located within the Eurasian temperate belt, characterized by hydrothermal or ecological conditions most favorable to forest growth.

The wide range of Siberian stone pine reflects a better ecological and geographical adaptability compared to other stone pines and many associated forest-forming species. Hence, in different parts of its range stone pine and its associated species form forest communities that are different in terms of species composition (depending on the landscape structure), specific natural and forest-site conditions, chorology, and many other properties.

REGIONAL DIFFERENTIATION

These spatial and geographical differences can be described as follows. The numbers refer to figure 1.

1. *Far north*: Most common forest communities are pre-tundra, open larch-spruce.

2. *Ural-Siberian*: Larch-spruce-stone pine forests in the Ural Mountains and western Siberia (*Larix sibirica* Lebed.) and in eastern Siberia *Larix dahurica* Turcz. and *Picea obovata* Lebed., including mountain birch (*Betula tortuosa* Lebed.), and white birch (*Betula pubescens* L.).

3. *Northern taiga subzone*: Spruce-stone pine forests with an admixture of fir (*Abies sibirica* Lebed.), white birch (*Betula pubescens* L.), drooping birch (*Betula ???*)

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

E. P. Smolonogov is Professor of Forestry, Institute of Forest, Ural Division of Russian Academy of Sciences, Bilimbayevskaya St. 32-A, 620134 Ekaterinburg, Russia.

dominating early phases of forest reestablishment and development, are very common.

4. *Middle and southern taiga subzones*: Fir-spruce-stone pine forests with the same birch species and aspen (at early successional phases) as the northern taiga.

5. *Foothills and on low mountains of southern Siberia*: Fir-stone pine forests with an admixture of spruce commonly occur. Birch species and aspen, same as those in the taiga, are typical during early phases of restoration and forest development.

6. *Northeast*: The stone pine range is dominated by specific light-demanding conifers of stone pine, Dahurian larch, and Scots pine (*Pinus sylvestris* L.). Asian white birch (*Betula platyphylla* Sukacz.) occurs at early phases of forest succession.

7. *Highlands of southern Siberia and the northern macroslope of the central Asian mountains (northern*

Mongolia): Larch-stone pine and pure stone pine forests occur with some admixture of spruces and white birches in the river valleys of the low mountains.

Natural conditions of the regional varieties of stone pine forests vary from region to region, but the variances can be explained by the differences in vegetation history and post-glacial landscape development, and thus in the character and intensity of biogeocenotic, soil-, and forest-formation processes. Naturally, the pathways of forest development and temporal changes in phytocenoses also vary.

REPRODUCTION AND AGE DYNAMICS

The most important forms of temporally changing forest communities can be described as follows:

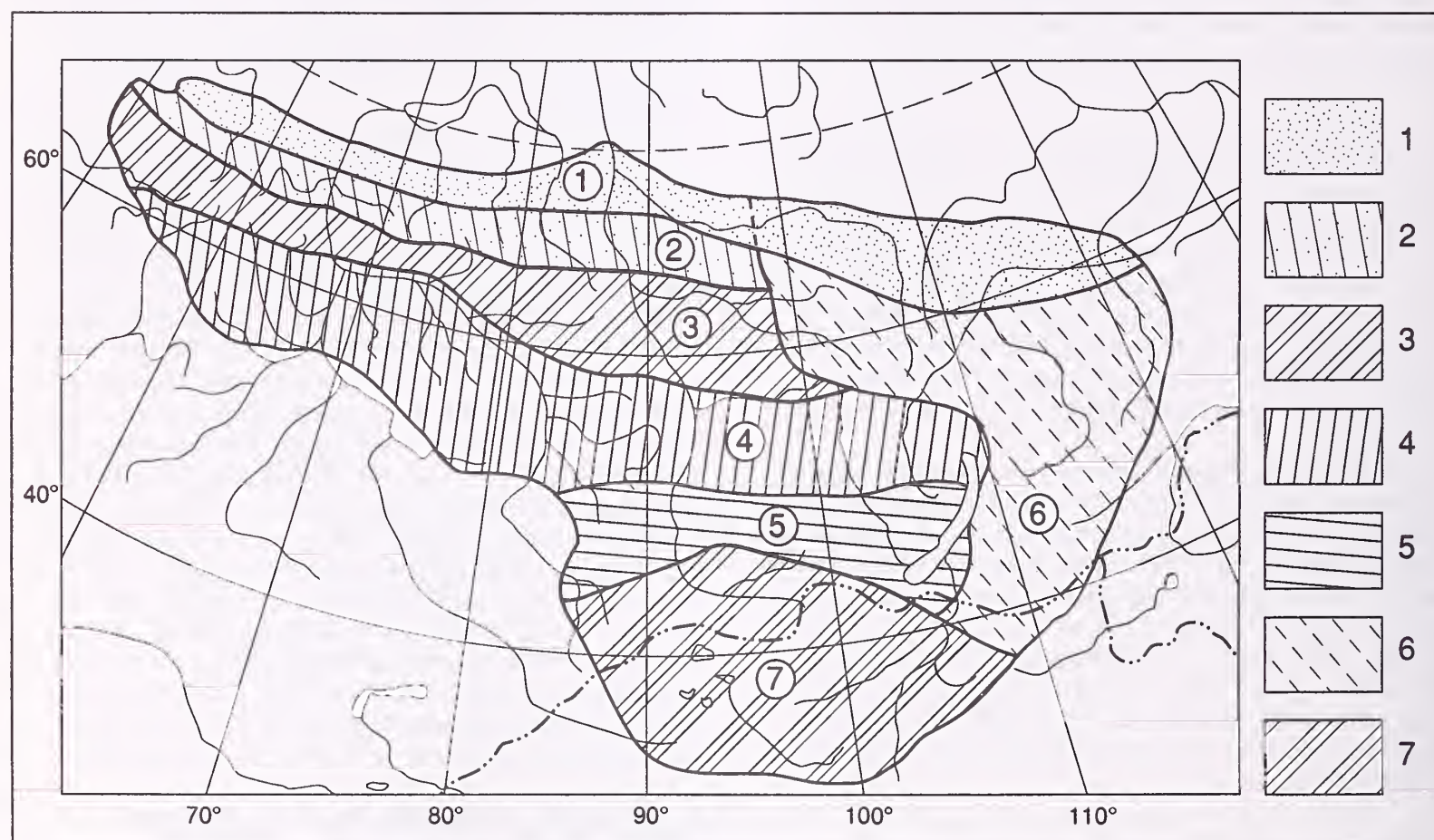


Figure 1—The range of Siberian stone pine and spread of forests with its admixture. 1—Far North: pretundra open larch-spruce forests; 2—Ural-Siberian: larch-spruce-stone pine forests (western Siberia: *Larix sibirica* Lebed.; eastern Siberia: *Larix dahurica* Turcz., *Picea obovata* Lebed.) including mountain birch (*Betula tortuosa* Lebed.) and white birch (*Betula pubescens* L.); 3—Northern taiga subzone: spruce-stone pine forests with additional fir (*Abies sibirica* Lebed.), white birch (*Betula pubescens* L.) and drooping birch and, sometimes, aspen (*Populus tremuloides* L.) dominating at early phases of forest stand and restoration, are very common; 4—Middle and southern taiga subzone: fir-spruce-stone pine forests with the same birch species and aspen (at early successional phases) prevail; 5—Foothills and low mountains of southern Siberia: fir-stone pine forests including spruce, birch species, and aspen; 6—Northeast: light-demanding conifer-stone pine forests with Dahurian larch and Scots pine (*Pinus sylvestris* L.). Asian white birch (*Betula platyphylla* Sukacz.) occurs at early phases of forest succession; 7—Highlands of southern Siberia and central Asian mountains: larch-stone pine and pure stone pine forests with some additional spruces and white birches in the river valleys of low mountains grow there.

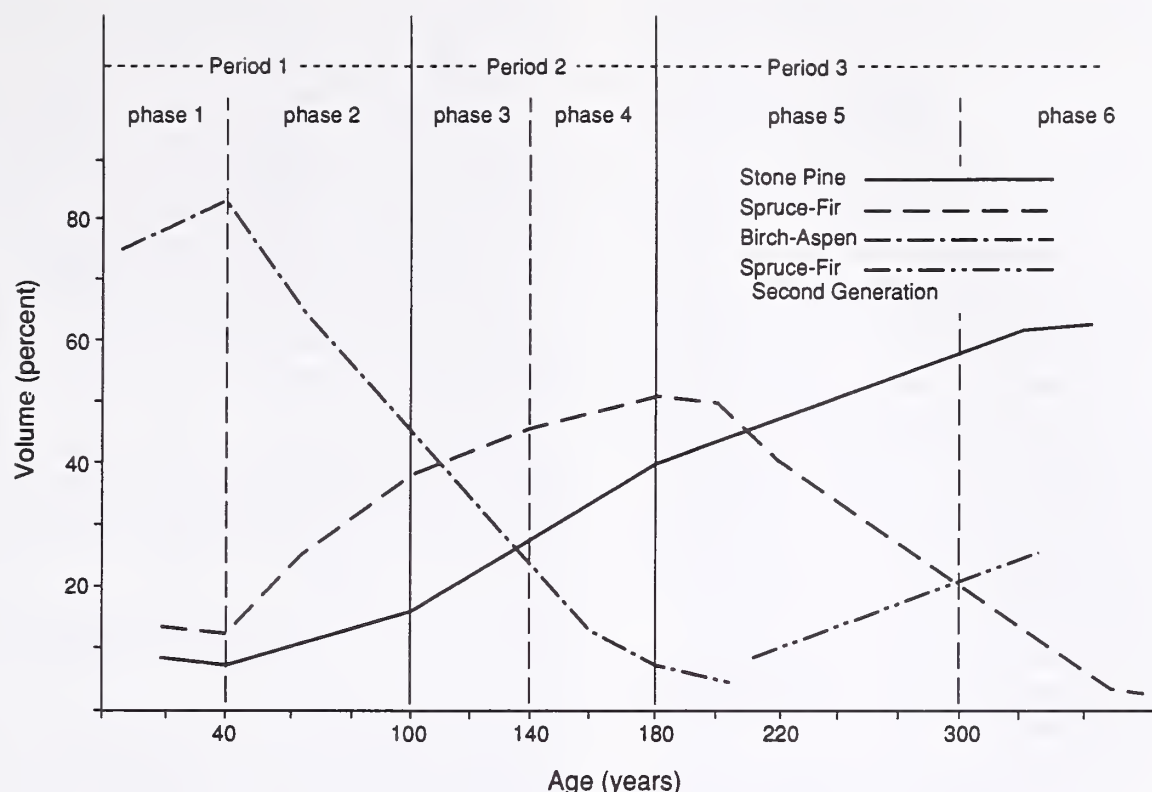


Figure 2—Reproduction-age dynamics scheme of modal stands in midtaiga, moss-herbaceous, hillside stone pine forests of the Trans-Urals submontane-plain forest site province. Stand admixture variation: 1—Siberian stone pine; 2—dark-coniferous species (Siberian spruce and fir); 3—deciduous species (birch, aspen); 4—second generations of dark-coniferous species.

- Age dynamics that characterize variation in phytocenoses (including alternation of age classes of woody plants) subject to a weak influence of external damaging factors in the course of long-term existence of the forest communities. Probably, climax forest communities can be formed.
- Reproduction and age-dynamics after fires that completely destroyed the forest on large areas. In this case forest succession starts again, and relatively even-aged stands are formed.
- Reproduction and age-dynamics after clearcut. Forest succession starts again, but now includes components of previous phytocenoses and some elements resulting from silvicultural management. A relatively even-aged stand is formed.

The first type of forest dynamics is typical of moist sites at low elevation, in depressions, and on hillsides moistened by outcropping water. The second type occurs all over the regions and is typical of fresh and dry sites. Stone pine forests of the Ural Mountains, Siberia, and central Asia were "fire-born." The third type is found in regions of intensive forest exploitation.

The successional behavior, formation, and temporal variation of stone pine forests in different regions have been intensively studied (Smolonogov 1990). Tree mensuration data were processed by the probabilistic-statistical method. The method derives biometric stand characteristics related to age classes, which are presented by computed growth curves for modal communities of each forest type studied. The "Ural version" of the genetic classification

(Kolesnikov and others 1974; Smolonogov 1990) served as the topological basis. It well reflects the altitudinal-orographic and latitudinal-zonal differentiation of forest sites and forest cover, while the forest type includes both natural and derivative (potential natural) forest communities growing in the same forest-site types. The stand is uneven aged, and forms the same natural-genetic development series. This approach to studying the dynamics is supported by the well-known concept that space succession may correspond to temporal succession of communities (Clements 1928).

The investigations show that a complete cycle of changes occurring during succession of forest communities that appear to have been heavily damaged is usually divided into three periods. The periods are subdivided into phases that follow each other in time and reflect quantitative and qualitative rhythms of the forest community development (morphocenogenesis). The age cycle of changes in each generation of community-forming ligneous plants can be broken down into ontocenogenesis stages.

A generalized reproduction-age dynamics scheme of one of the types of mountain stone pine forests of the northern Urals is shown in figure 2:

First Period—Restoration and formation of stone pine forests dominated by rapidly growing deciduous species (birch, aspen). Stone pine and spruce and fir (the latter ones are species of the dark taiga) are growing in the lower stories of the biogeocenoses. Potential stone pine-deciduous communities (actually young stone pine growth) are formed in this period. The period lasts for 80 to 100

years. It is subdivided into two phases. The first phase (1) is characterized by natural reproduction and formation of deciduous young growth and stone pine undergrowth. During the second phase (2) the upper deciduous story is stabilized and its degradation begins. Spruce, fir, and stonepine grow in the understories of the communities.

Second Period—Formation of stone pine forests subject to the influence of prevailing and forest-forming spruce and fir. Stone pines form the second layer, while rapidly growing trees prevail in the upper story, where stone pines may account for up to 20 to 30 percent of the growing stock. During this period taiga develops that is a potential stone pine forest (actually a medium-age stone pine forest). The period lasts for 80 to 100 to 160 to 180 years and also is subdivided into two phases. During the first phase (3), the upper story, which is dominated by dark-taiga coniferous species is formed. The second phase (4) is characterized by stabilization of economically mature spruce and fir forest, high seed production of all forest-forming species, initial mortality first of fir and then of spruce, and then the appearance of second-growth generations of dark-taiga coniferous trees and stone pine.

Third Period—Stabilization and natural maturity of stone pine forests. This period begins after 160 to 180 years and persists 400 years and longer. Stone pine is dominant, its share in the canopy layer amounts to 30 to 100 percent. First the lower layer of woody plants and

then the medium layer comprising second-growth generations are formed in this period. The period can be divided into two phases: In the first phase (5), stone pine forests are stabilized, and the increment of merchantable timber is at its maximum. Stone pine is producing maximum amounts of seed, and the mortality of old fir and spruce trees continues. The second phase (6) is characterized by maturity of stone pine forests, decrease in seed production, gradual degradation of the older (first) canopy layer, and then the formation of the main story by younger generations of dark-taiga coniferous trees and stone pines. Phase duration varies between 280 to 300 to 400 to 450 years, and more.

Sometimes a third phase becomes apparent, when a few old, large-sized stone pines dominate the canopy layer, while the main forest story is formed by second and younger generations of deciduous trees, spruce, fir, and stone pine. The proportion of stone pine in forest composition is different in various regions and forest sites. In pretundra forests, in subzones of northern and partially middle taiga of western Siberia, in mountain stone pine forests of the Ural Mountains, and on fresh sites, stone pine is very common in second-generation stands. Under humid conditions in the moist sites of the middle and southern taiga, and in the foothills and low-elevation areas of the Altai-Sayan mountain system, stone pine forests are often replaced by spruce and fir forests.

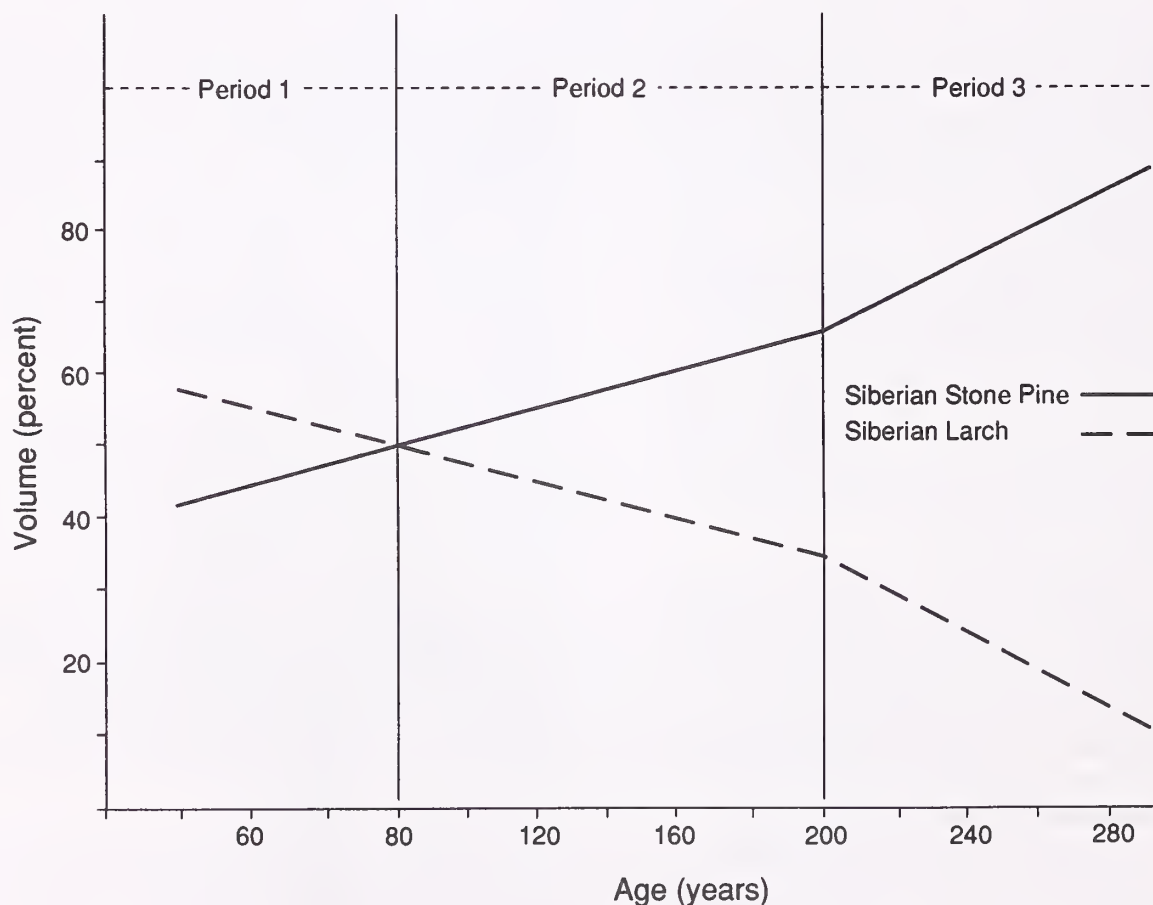


Figure 3—Reproduction-age dynamics scheme of reedgrass-vaccinium, stone pine forests on the northern macroslope of eastern Tannu-Ola (Tuva-northern Mongolia). Stand admixture variation: 1—Siberian stone pine; 2—Siberian larch.

The regularities described here in reproduction-age dynamics are surely far from reflecting the whole variety observed in nature, but they are clearly determined by ecological-geographical factors. For example, figure 3 illustrates reproduction-age dynamics of a stone pine forest with additional larch, located on the northern slope of eastern Tannu-Ola (at the Russian-Mongolian border). However, despite all this there also are general regularities, which are presented in the generalized scheme. They are due to the most essential ecological-biological properties of stone pine, the major forest-forming species. These stone pine characteristics include seed dispersal by animals (strongest relationship with *Nucifraga caryocatactes macrorhynchos* Br.), relative shade tolerance at early stages of existence, accelerated growth and development under favorable light conditions, and a much longer life span than other forest-forming species.

FOREST MANAGEMENT IMPLICATIONS

An analysis of forest management materials shows that the regularities in the reproduction-age dynamics are not adequately considered in forest management. Stands of the initial period are usually taken for deciduous forests, and those of the second period as spruce and fir forests, with management norms assigned correspondingly. This leads inevitably to an artificial alternation of tree species, to cutting of actually young and middle-aged stone pine forests. All the investigation data suggest the need for an integrated stone pine forestry program, which would combine potential stone pine-deciduous forests of the first period, spruce and fir forests of the second period, and stone pine forests of the third period. Thus, a strategic basis for the development of a management system could be created.

If this basis is not available, the areas covered with stone pine forests will surely continue to shrink.

REFERENCES

- Bobrov, E. G. 1974. Coniferous breeds of USSR. Nauka. 212 p. [In Russian].
- Clements, F. E. 1928. Plant succession and indicators. New York: Hafner Publishing. 453 p.
- Kolesnikov, B. P. 1956. Stone pine of forests in Far East. Publ. Academy of Sciences of USSR. 264 p. [In Russian].
- Kolesnikov, B. P.; Zubareva, R. S.; Smolonogov, E. P. 1974. Forest-site conditions and forests types in Sverdlovsk's region. Publ. Ural Division of Academy of Sciences USSR. Sverdlovsk. 176 p. [In Russian].
- Krylov, G. V. 1961. Forests in west Siberia. Publ. Academy of Science of USSR. 255 p. [In Russian].
- Luzganov, A. G.; Abaimov, A. P. 1977. Role of river basins and wind in spreading and evolution of larch, stone pine and others forest breeds. Publ. Siberian Technological Institute. 8: 31-38. [In Russian].
- Neishtadt, M. I. 1957. History of forests and paleogeography of USSR in holocene. Publ. Academy of Sciences of USSR. 404 p. [In Russian].
- Nepomilueva, N. I. 1974. Siberian stone pine (*Pinus sibirica* Do Tour.) in north-east of European part of USSR. Nauka. 184 p. [In Russian].
- Smolonogov, E. P. 1990. Ecological and geographical differentiation and dynamics of Siberian stone pine forests in Ural and plains of West Siberia. Publ. Ural Division of Academy of Sciences of USSR. Sverdlovsk. 286 p. [In Russian].
- Smolonogov, E. P.; Vegerin, A. M.; Kolesnikov, B. P. 1970. Forest-site zones in Tumen's region—botanical researches in Ural. Publ. Ural Division of Academy of Sciences of USSR. Sverdlovsk: 34-58. [In Russian].

THE CEMBRAN PINE IN THE FRENCH ALPS: STAND DYNAMICS OF A CEMBRAN PINE FOREST IN TUEDA (SAVOY, FRANCE)

Lise Wlérick

Abstract—In the Tueda Natural Reserve (Savoy, France), the most important northern French cembran pine stand, a study of stand structure dynamics was started in mixed stands of spruce (*Picea abies*) and cembran pine (*Pinus cembra*). Six types of stand structures were established on the basis of the following main criteria: spruce and cembran pine ratio, extent of canopies, and regeneration and diameter classes. The stands are very young.

Cembran pine (*Pinus cembra* L.) has been heavily over-exploited in France. Nowadays it can only be seen in marginal areas with an often-limited accessibility. Queyras (Hautes Alpes) and Maurienne (Savoy), however, still possess beautiful cembran pine stands. In the north, cembran pine is often scattered. Nevertheless, in the Tueda forest (in the Allues Parish) the most remarkable cembran pine stand exists in the northern French Alps.

Its importance and specificity led us to study it more closely. The possibility of a future intervention encouraged us to learn about its history, its characteristics, and its stand dynamics.

FRENCH CEMBRAN PINE STANDS

Cembran pine is present throughout the Alps from the Mediterranean Sea to eastern Austria (Contini and Lavarello 1982). It grows mainly in the Alpine Region but can also be found in the Carpathian Mountains and the Transylvanian Alps. In the Alps, cembran pine can only be found in Austria, France, Italy, and Switzerland. The amount of cembran pine stands varies from one country to another, and occurs in the following decreasing order:

- 19,400 ha in Italy (Del Favero and others 1985).
- 15,600 ha in Austria (Contini and Lavarello 1982).
- 12,400 ha in France (Contini and Lavarello 1982).
- 11,900 ha in Switzerland (National Forestry Inventory).

These figures come from the National Forestry Inventories.

The distribution of cembran pine is mostly contiguous in Austria, Italy, and Switzerland; in France it is sporadic. This is essentially due to strong human influences.

History

Where cembran pine grew in the upper part of the forests, it was often eliminated to create meadows and allow grazing. Larch (*Larix decidua* Miller), on the other hand, with its less dense canopy could shelter animals as well as let them graze the grass under it. Despite the fact that larch grows at the same altitude as cembran pine, it suffered less from human impact than the latter.

Upper montane and subalpine belt forests were subjected to fire and excessive deforestation and logging. Much wood was used for cooperage (wooden casks), millwork, cabinet-work, and wood carving (Contini and Lavarello 1982).

The decrease of cembran pine is mainly due to human influence. Palynological studies in French alpine peatlands reveal old cembran pine occurrences outside its present range. Fourchy (1986) cited the cembran pine occurrence of Pelleautier west of Gap; Bartoli (1966) mentioned an occurrence in the peatlands in the Valmeinier Valley in High Maurienne as well as another one in areas above Thyl, which are treeless now.

Within its present distribution area, cembran pine mainly occurs on northern and steep slopes. On the southern slopes, only a few cembran pines are left, since those areas were traditionally preferred to build houses and for farming and grazing, just as on gentle slopes. The Versant du Soleil above La Cote d'Aime in Tarentaise is an excellent example of this use of space.

The distribution of cembran pine must have been at its maximum 3,000 or 4,000 years ago, before humans started substantial deforestation (Combes 1986). Mountain populations began to decrease after 1850 (Ozenda 1985). The consequences of this change on logging, fire, and pasture became obvious between 1860 and 1880, according to departments. An increase of cembran pine in subalpine heaths and in areas no longer used for grazing has been observed for more than 40 years. At present, we observe a great vitality of cembran pine, which is spreading horizontally and to lower elevations (Maurienne: 1,100 m; Tarentaise: 1,300 m), often far from seed-bearing trees. It does not extend much to higher elevations.

Natural Environment

Cembran pine extends from the Alpes Maritimes to the Haute Savoie. Its distribution is roughly the same as that of larch (fig. 1), except for two main differences: in the northern Alps its western boundary greatly overlaps the

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Lise Wlérick is a Forester, National Forestry Office, Technical Division, 73200 Albertville, France.

larch distribution while, in the southern Alps, larch goes farther south than cembran pine (Fourchy 1986). However, Combes (1986) showed in the Alpes of Haute Provence the cembran pine spread farther south than Fourchy found it.

We can divide Alps into three parts: Pre-Alps, Intermediate Alps, and Intra-Alpine Alps. Pre-Alps can be characterized by the widespread natural distribution of beech (*Fagus sylvatica* L.) and by the absence of larch growing naturally; the Intra-Alpine axis by natural occurrence of larch and the absence of beech; and the Intermediate Alps by the co-existence of natural larch with natural beech. According to these definitions, in the northern Alps cembran pine reaches the Pre-Alps with cembran pine stands spread out from

1,500 to 2,000 m of altitude, while isolated or stunted trees occur from 1,300 to 2,000 m of altitude. In the southern Alps, cembran pine is limited to Intra-Alpine and Intermediate Alps; stands are spread out from 1,800 to 2,200 m of altitude, stunted or isolated trees from 1,100 to 2,480 m. A recolonization of this species particularly at lower altitudes has been observed in recent years (Tarentaise, Maurienne).

All exposures are fit, but a clear preference for cool exposures (northern and neighboring) is known. It is not obvious whether this distribution is due to ecology or to human influence (more important in sunny exposures) (Fourchy 1968).

Cembran pine can grow on any geological substrata and more favorably on siliceous rocks: gneiss, granite, sandstone, flysch, schist, etc. It can, however, be found on gypsum in La Plagne (Tarentaise) or limestone in Flaine (Fourchy 1968) and on gypsum and limestone in Termignon and Bramans (Maurienne) (Bartoli 1966). Sites on limestone are usually rather marginal.

We can differentiate hygrophilous subseries from xerophilous subseries within communities. The hygrophilous subseries characterized by *Pinus cembra*, *Rhododendron ferrugineum*, *Lonicera caerulea*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Calamagrostis villosa*, etc., which can be separated into four facies: *Vaccinium myrtillus* facies, *Geranium sylvaticum* facies in coomb, *Calamagrostis villosa* facies, and *Pinus uncinata* facies, with *Erica herbacea*, *Sorbus chamaemespilus*, etc., on limestone. The xerophilous subseries differs in the presence of *Juniperus nana* and *Arctostaphylos uva-ursi*.

Along the subalpine belt two ecological situations can be observed, one on the northern slope and one on the southern slope. These coincide with two heath types, one of *Rhododendron-Vaccinium* and the other of *Juniperus-Arctostaphylos*, respectively, and are liable to afforest in one or the other of the four tree species: cembran pine, larch, mountain pine (*Pinus uncinata* [DC]), and spruce (*Picea abies* [L.]) (Ozenda 1985).

In the northern Alps the former situation prevails. The climate is wetter, and as a result the difference in exposure between the south-facing slope and the north-facing slope is less perceptible than in the southern Alps—moisture is rarely a limiting factor. Therefore, cembran pine stands, or cembran pine stands with larch, represent the most prevailing types and that xerophilous type tends to be limited to the southern slopes.

Structure and Dendrometrics

In France, it is uncommon to see pure cembran pine stands, such as those seen in the Engadine or Tyrol (Fourchy 1968). We find this pine often associated with spruce or mountain pine in Pre-Alps and with larch or mountain pine in the Intra-Alpine axis. French National Forestry Inventory reports, in decreasing order, the associate species of cembran pine (Contini and Lavarello 1982):

Species	Percent
Larch	86.0
Spruce	30.0
Mountain pine	15.0
Scots pine	10.0
Fir	9.0
Various broad-leaved trees (aspen, alder, birch)	4.5

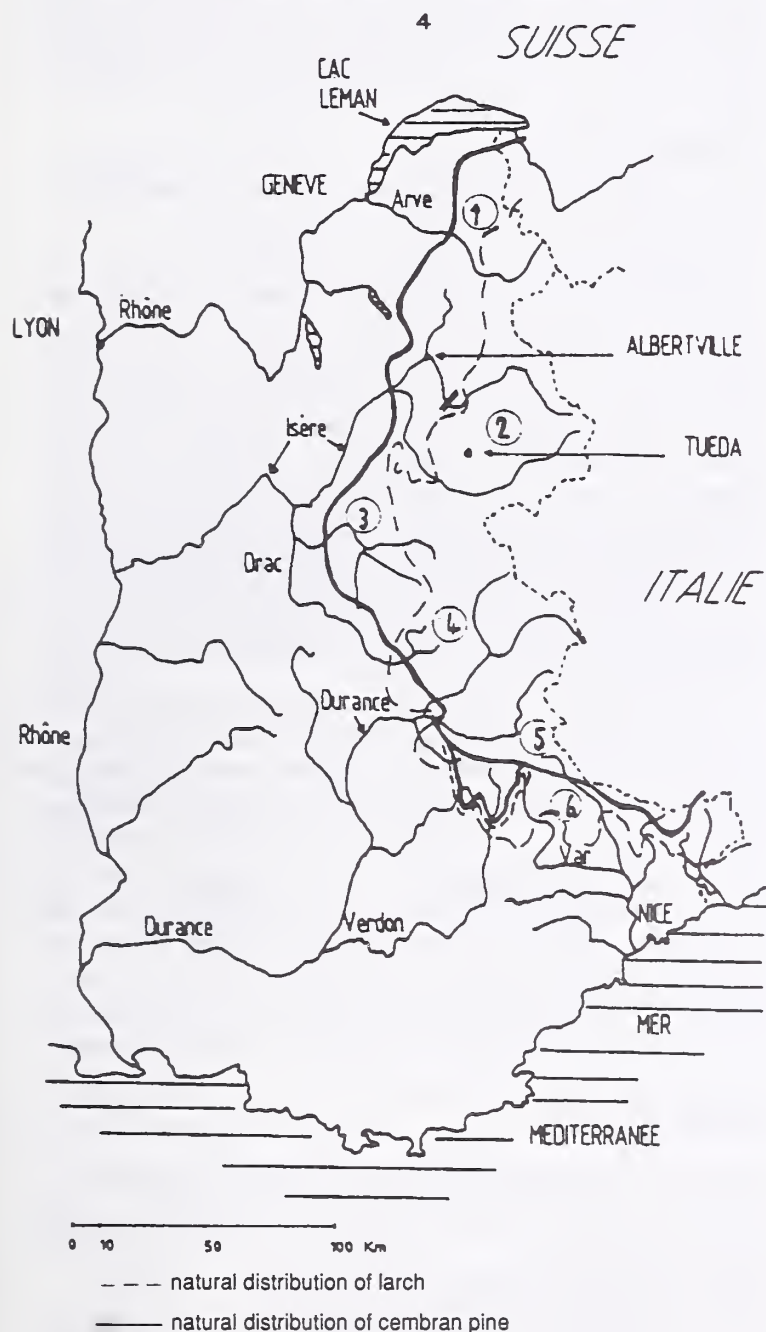


Figure 1—Distribution of cembran pine and larch in the French Alps (Fourchy 1968). 1—Haute Savoie; 2—Savoie; 3—Isère; 4—Hautes Alpes; 5—Alpes de Haute Provence; 6—Alpes maritimes. According to my personal observation, the boundary of larch has been modified in Tarentaise (====) just like that of cembran pine in Alpes de Haute Provence as mentioned in Combes (1986) (— — —).

Cembran pine stands usually have sparse canopies. Stand density is often less than 200 trees/ha with a mean at the same elevation of 135 trees/ha (Contini and Lavarello 1982). Other species have higher stand densities. Standing volume per hectare is also low (35 m³/ha on the average).

Structure of natural stands is always an irregular clump forest. It is interesting to note that even in the case of high stand density, we have the same type of structure: clumps separated by small openings whose width is about one to three times as much as the average diameter of the crown of the biggest trees (Contini and Lavarello 1982).

Cembran pine very easily colonizes lands abandoned by grazing and human activity; it also regenerates well under clear stands. On the other hand, it does not regenerate easily under denser crown cover.

DYNAMICS OF THE TUEDA STAND

The cembran pine stand of Tueda constitutes a remarkable upper altitude ecosystem, with respect to ecology and landscape, on the outskirts of Vanoise National Park in the Allues Parish (also see fig. 1 for its location). It has been managed by the National Forestry Office since 1989, and jointly with the National Park of Vanoise since 1990, when the Natural Reserve of Tueda, which includes the entire stand, was established. The National Forestry Office manages about 600 ha out of the 1,100 ha of the natural reserve.

Of the 600 hectares there are 150 ha of more or less dense pure cembran pine stands in the upper part and mixed cembran pine and spruce stands in the lower part (Pignol 1992). These stands range from 1,670 to 2,220 m in altitude. Above 1,900 to 2,000 m altitude, spruce is rarer and varies by exposure. The forest is essentially rooted in acid rocks (schist, sandstone, gneiss) (Pignol 1992). This area, which has been grazed for a long time by cows and goats, is still grazed today, though less extensively than before.

We estimate that the cembran pine stand will eventually extend to about 400 ha. That is 400 ha of land which will become forest depending on how rapidly grazing disappears and if humans do not intervene.

Patches, which were private until 1969, have not been logged since that time. However, when the patches were bought by the village council, a lot of large-size trees had already been logged by the owners. Apart from a few windthrows, the forest, which is young, is getting older. As meadows and pastures become afforested, cembran pine and spruce seedlings quickly colonize open spaces, and the pressure of grazing is not strong enough to fight this phenomenon.

At present there is an interesting balance in the landscape between the more or less clear stands, the pastures, the meadows, the *Alnus viridis* bushes, *Rhododendron* and *Juniperus* heaths, and fallen rocks.

Study Purposes

The cembran pine stand of Tueda is the most important northern cembran pine stand in France. What is interesting is that it is a young stand. Recent pollen analyses have confirmed the absence of larch and mountain pine. The association of cembran pine with spruce to such a large extent

is unique in France and very rare in Europe (a few stands in Italy and Austria).

Besides being a very rare occurrence in the French Alps, the relict cembran pine stand of Tueda also offers the advantage of presenting side by side two typical associations of cembran pine on three different exposures (southwest, north, northeast):

- the hygrophylous subseries with *Rhododendron ferrugineum* and *Vaccinium myrtillus*.
- the xerophylous subseries with *Juniperus nana*.

Besides the usual varied mountain flora, the cembran pine stand of Tueda contains the most luxuriant *Linnaea borealis* site of the six French sites, all found in Savoy. *Linnaea borealis* is a true boreal pine relict protected at the national level. We also find a lot of wet sites with peatlands and protected flowers such as *Stemmacantha rhapsantica*, *Clematis alpina*, *Primula farinosa*, *Swertia perennis*, *Carex microglochin*, and *Carex bicolor*.

Wildlife is just as rich. We observe nutcrackers, black grouse, golden eagles (which nest there), rock partridge, and ptarmigan, as well as many other species.

To manage this natural area with the aim of preserving or improving its biodiversity and guaranteeing an always attractive landscape for the many visitors who walk through it in summer and in winter, we wish to know better the stand dynamics. We thus are studying the natural growth of the existing stands as well as the competition between cembran pine and spruce. We also are studying the mechanisms of the closing of present openings and the rising of the timberline, which seem to be linked to the presence of the nutcracker, a bird that favors the scattering of seeds. We will obtain information that will allow us to decide whether it is necessary to intervene or not in this sensitive natural area, and if we do, how.

Cembran pine, a noble coniferous species used for wood-carving and cabinetwork, has been heavily overexploited up to now. This is a much-prized species from an economic and cultural point of view. Its price is five times as high as that of spruce.

Many forests in Tarentaise and in Maurienne, as well as in the rest of the Alps, are likely to be favorable for the natural development or forestry planting of cembran pines. The study of the cembran pine stand of Tueda will also be of great use for other cembran pine stands (present or potential) in Savoy, both in the French Alps and the rest of Europe.

Methodology

A forest management plan was established in 1991. On that occasion the vegetation, stand and regeneration mapping was carried out.

Four types of stands were distinguished:

- pure cembran pine stands with 5 to 40 percent canopy and with >40 percent canopy.
- mixed spruce and cembran pine stands with 5 to 40 percent canopy and with >40 percent canopy.

For regeneration, the presence of cembran pine and spruce seedlings was noted both under crown cover or beside it.

These mappings allowed us to develop a statistical inventory in the mixed spruce and cembran pine stands in

1992. One plot with 5 are/ha (1 are = 100 m²) was counted in a systematic grid. In total 75 plots were computed. The following data and measurements were taken:

- environment data: altitude, exposure, main vegetation, presence or absence of falling rocks.
- dendrometrical data: (1) inventory of all trees over 7.5 cm diameter by species and by diameter classes; (2) sample basal area; (3) on the three trees nearest to the center of the plot: width of the last 10 rings, age at 1.30 m, diameters of crown projection (maximum diameter and diameter perpendicular to the maximum diameter), total height, height to first live branch.
- morphological data: stand structure over 25 ares (total height was considered as absolute height).

The maximum height was estimated to be 24 m. Thus the creation of four height strata:

Height (m)	Strata
24	Stratum 1
18	
12	Stratum 2
6	Stratum 3
0	Stratum 4= regeneration

The ratios of strata 1, 2, and 3 have been noted in 1.10^{-1} .

Three categories of diameter were defined: small-size trees (PB) $10 \text{ cm} \leq \phi \leq 20 \text{ cm}$; medium-size trees (BM) $25 \text{ cm} \leq \phi \leq 25 \text{ cm}$; large-size trees (GB) $\phi \geq 40 \text{ cm}$.

The ratios of these three categories of diameter have also been given:

- Presence of openings covering a surface of at least 10 ares out of 25 ares have been noted in 1.10^{-1} .
- Presence and abundance of regeneration over 5 ares have been classified in four groups:

Group	Regeneration
0	none
1	very diffuse
2	scattered
3	abundant

The ratio between spruce and cembran pine regeneration also has been noted in 1.10^{-1} .

- Windthrow number over 5 ares for spruce and cembran pine.
- Stump number over 5 ares.
- Canopy (crown projection of strata 1, 2, and 3 in ratio at the total surface of the plot) over 5 ares in 1.10^{-1} .

Data Processing and Results

A first principal component analysis has enabled us to leave out the nonsignificant variables and those that are too correlated. Sixteen variables out of 29 have thus been kept for the second principal component analysis. They can be found in figure 4. The first three main axes of the second

principal component analysis account for 61.3 percent of the inertia of the phenomenon. The first main axis accounts for 29.6 percent of the total variation, the second one for 17.8 percent, and the third one for 13.9 percent. These results are satisfactory (Leclerc 1992).

A hierarchical ascending classification then enabled us to determine six different types of stands and to draw up a determination key.

Group N°1 is characterized by a very high percentage of cembran pine (91 percent of the number of trees), a medium canopy ($5.4 \cdot 10^{-1}$), very low regeneration, very few small-size trees ($0.8 \cdot 10^{-1}$), quite a few large-size trees ($5.3 \cdot 10^{-1}$), and an average number of medium-size trees ($3.9 \cdot 10^{-1}$). It can be assimilated to an irregular cembran pine clump forest, with large- and medium-size trees and of average stand density, in which large-size trees clearly predominate.

Group N°2 is characterized by a higher proportion of spruce, which however remains moderate (55 percent of the number of trees), an important canopy ($7.7 \cdot 10^{-1}$), an average rate of regeneration in which spruce predominates, quite a balanced distribution of small-size, medium-size, and large-size trees (respectively, $4.0 \cdot 10^{-1}$; $3.6 \cdot 10^{-1}$; $2.4 \cdot 10^{-1}$). It looks like a selection forest of cembran pine and spruce in which spruce predominates.

Group N°3 has a very high percentage of cembran pine (84 percent of the number of trees), but it differs from Group N°1 by a less dense canopy ($3.6 \cdot 10^{-1}$), regeneration exclusively composed of rather scattered cembran pine seedlings, a hardly marked predominance of medium-size trees ($4.5 \cdot 10^{-1}$), a not inconsiderable number of large-size trees ($3.9 \cdot 10^{-1}$), and few small-size trees ($1.6 \cdot 10^{-1}$). It is quite similar to an irregular cembran pine clump forest with medium and large trees, of low stand density, but with a predominance of medium-size trees and rather diffused regeneration of cembran pine.

Group N°4 is also characterized by a high percentage of cembran pine ($7.4 \cdot 10^{-1}$ of the number of trees), a limited canopy ($3.5 \cdot 10^{-1}$), rather diffused regeneration of spruce and cembran pine, a predominance of small-size trees ($6.0 \cdot 10^{-1}$), a limited proportion of medium-size trees ($2.9 \cdot 10^{-1}$), and few large-size trees ($1.1 \cdot 10^{-1}$). It looks like a mixed spruce and cembran pine clump forest, but with a predominance of cembran pine, of low stand density, with a diffused regeneration of spruce and cembran pine, rather regular in its small-size trees. Altitude is between 1,680 and 1,850 m.

Group N°5 differs from Group N°4 in that it is located at a higher altitude, from 1,780 to 1,950 m. Moreover, the regeneration is abundant, with a predominance of cembran pine. The canopy is of medium density ($4.5 \cdot 10^{-1}$), the proportion of cembran pine is high (77 percent of the number of trees), and the small-size trees largely predominate ($7.1 \cdot 10^{-1}$). It can be assimilated into a regular cembran pine forest of small-size trees, with medium stand density and abundant regeneration.

Group N°6 is very different from the other groups. The proportion of spruce is very important (86 percent of the number of trees). So are the canopy ($9.5 \cdot 10^{-1}$) and the proportion of small-size trees ($7.8 \cdot 10^{-1}$). However, these small-size trees are distributed over two height strata, stratum 3 (6 to 12 m) and stratum 2 (12 to 18 m). Regeneration is of course limited for this group, which is similar to a very dense spruce stand, with very regular small-size trees.

To illustrate all this, the characteristics of groups 1 and 6 are given in figures 2 and 3.

The factorial discriminant analysis has enabled us to bring out the correlations between the variables (fig. 4).

Observations	Spruce and cembran pine		Spruce (sp)		Cembran pine (cp)	
* g calculated	Average altitude (m) = 1.740		Spruce regeneration (1/10) = 0		Cembran pine regeneration (1/10) = 1.4	
	Canopy	(1/10) = 5.4	N sp/ha	= 28	N cp/ha	= 274
	Stratum 1 (24-18 m)	(1/10) = 1.9	g sp (m ²) *	= 3	g cp (m ²) *	= 36.4
	Stratum 2 (18-12 m)	(1/10) = 5.4	V sp (m3/ha)	= 22.5	V cp (m3/ha)	= 205.3
GB = $\phi \geq 40$ cm	GB	(1/10) = 5.3	GB sp (1/10)	= 4	GB cp (1/10)	= 4.4
BM = $25 \text{ cm} \leq \phi \leq 35$ cm	BM	(1/10) = 3.9	BM sp (1/10)	= 2	BM cp (1/10)	= 4.3
PB = $10 \text{ cm} \leq \phi \leq 20$ cm	PB	(1/10) = 0.8	PB sp (1/10)	= 4	PB cp (1/10)	= 1.3
Regeneration code	Regeneration (code)	= 0.1	% sp in number of trees	= 9	% cp in number of trees	= 91
0 = no regeneration	Total number of trees/ha	= 302	% sp in g	= 8		
1 = very diffuse	g (m ²) sample basal area	= 17.2				
2 = scattered						
3 = abundant						

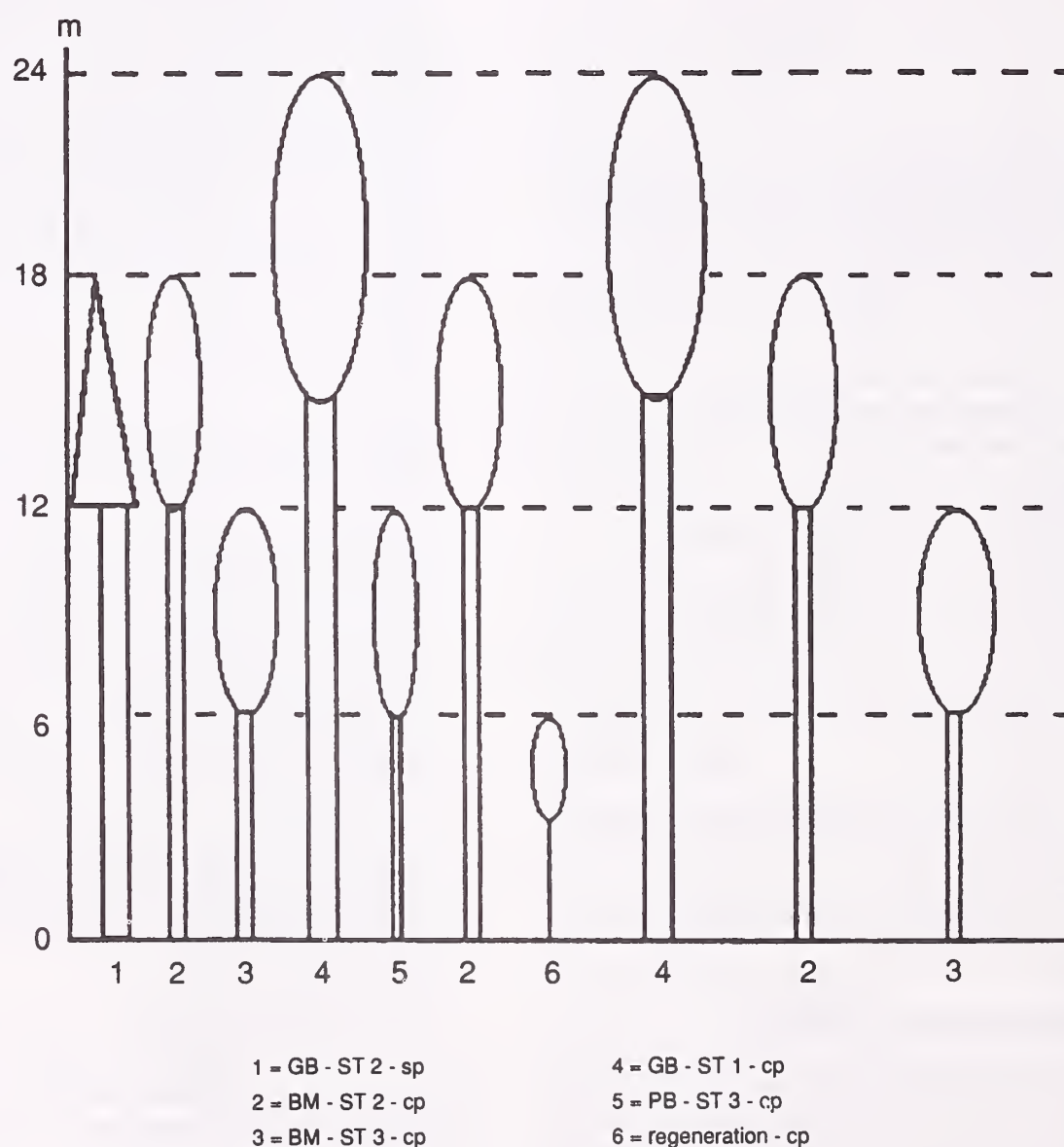
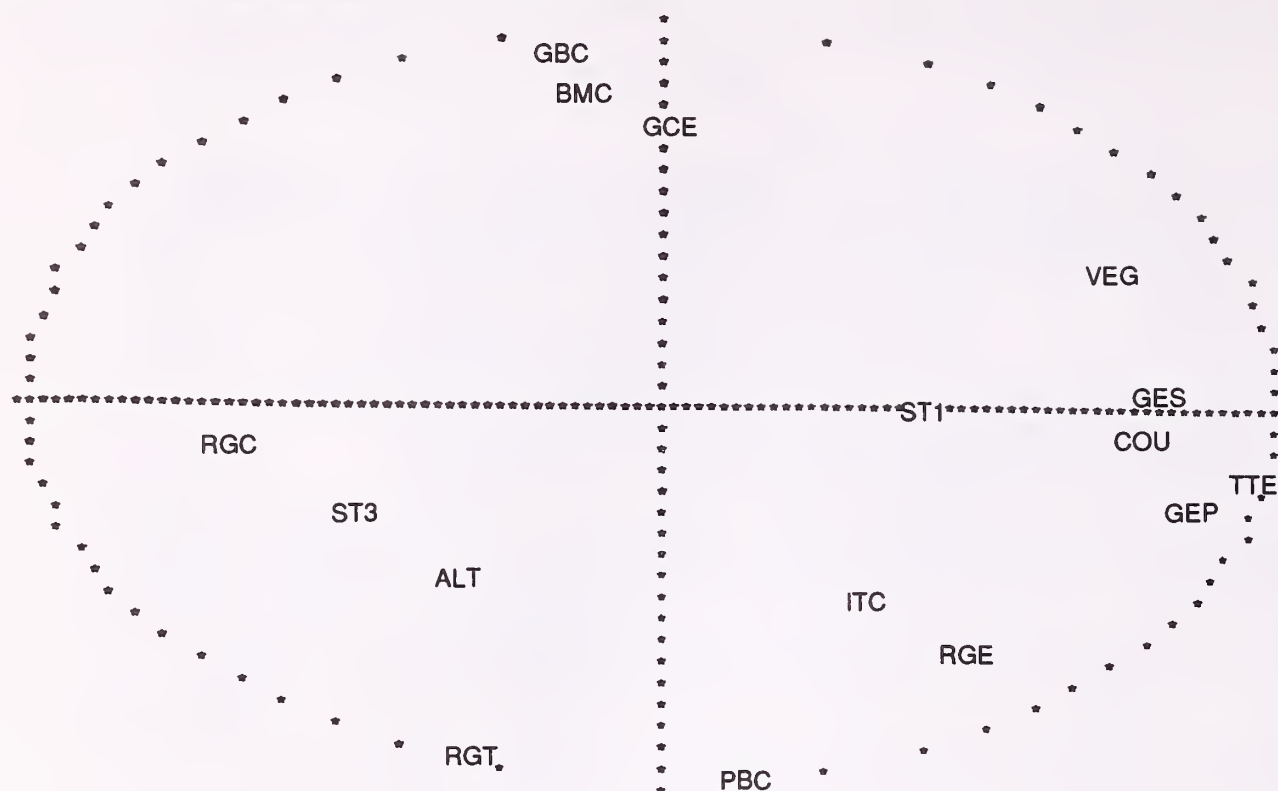


Figure 2—Group 1: Characteristics and diagram.

Observations	Spruce and cembran pine	Spruce (sp)	Cembran pine (cp)
* g calculated	Average altitude (m) = 1.815	Spruce regeneration (1/10) = 4.5	Cembran pine regeneration (1/10) = 0.5
	Canopy (1/10) = 9.5	N sp/ha = 1,880	N cp/ha = 310
	Stratum 1 (24-18 m) (1/10) = 1	g sp (m ²) * = 56.5	g cp (m ²) * = 9
	Stratum 2 (18-12 m) (1/10) = 4	V sp (m3/ha) = 328.3	V cp (m3/ha) = 33.2
GB = $\phi \geq 40$ cm	GB (1/10) = 0.4	GB sp (1/10) = 0.4	GB cp (1/10) = 0.6
BM = $25 \text{ cm} \leq \phi \leq 35$ cm	BM (1/10) = 1.8	BM sp (1/10) = 1.9	BM cp (1/10) = 1.0
PB = $10 \text{ cm} \leq \phi \leq 20$ cm	PB (1/10) = 7.8	PB sp (1/10) = 7.7	PB cp (1/10) = 8.4
Regeneration code	Regeneration (code) = 0.5	% sp in number of trees = 86	% cp in number of trees = 14
0 = no regeneration	Total number of trees/ha = 2,190	% sp in g = 86	
1 = very diffuse	g (m ²) sample basal area = 34		
2 = scattered			
3 = abundant			



Figure 3—Group 6: Characteristics and diagram.



- ALT : altitude
 VEG : vegetation
 COU : canopy of strata 1, 2 and 3 in 1.10^{-1}
 GES : sample basal area
 RGT : total regeneration (spruce and cembran pine)
 ST1 : importance of stratum 1 (18-24 m) in 1.10^{-1}
 ST3 : importance of stratum 3 (06-12 m) in 1.10^{-1}
 PBC : ratio of small-size trees calculated ($10 \text{ cm} \leq \phi \leq 20 \text{ cm}$) in 1.10^{-1}
 BMC : ratio of medium-size trees calculated ($25 \text{ cm} \leq \phi \leq 35 \text{ cm}$) in 1.10^{-1}
 GBC : ratio of large-size trees calculated ($\phi \geq 40 \text{ cm}$) in 1.10^{-1}
 RGE : spruce regeneration in 1.10^{-1}
 TTE : number of spruce trees over 5 ares
 GEP : spruce basal area
 RGC : cembran pine regeneration in 1.10^{-1}
 TTC : number of cembran pine trees over 5 ares
 GCE : cembran pine basal area

Figure 4—Variables correlation circle (Factorial Discriminant Analysis).

In figure 4, the first principal axis represents the growing stock:

- In the positive part of the axis, it is closely linked to the total number of spruce, to the spruce basal area, to the total canopy, and to the total sample basal area.
- In the negative part of the axis, it is closely linked to the cembran pine regeneration and to stratum 3 (6 to 12 m) (Leclerc 1992).

The second principal axis represents the individual height of trees:

- In the positive part of the axis, it is strongly correlated with the ratio of large-size trees and of medium-size trees as well as with the cembran pine basal area.

- In the negative part of the axis, it is strongly correlated with the small-size trees ratio (Leclerc 1992).

In figure 5, we can observe the position of individuals as well as that of the six groups. Ninety-six percent of the individuals have been well classified in the factorial discriminant analysis.

In the forest management plan of Tueda, Pignol (1992) showed that the mixed spruce and cembran pine stands had a canopy ranging from 5 to 40 percent in only 12 percent of cases—their canopy was over 40 percent otherwise. On the other hand, in the pure cembran pine stands that we have not fully studied yet, the opposite can be observed: over 40 percent of the canopy can be found in 25 percent of the area.

So, in the cembran pine forest of Tueda, we can find analogies with the other French cembran pine stands. Yet it presents notable characteristics, among which is its youth.

New And Future Studies

In our study of mixed spruce and cembran pine stands, we have not yet been able to analyze all the data concerning the growth, age, and crown shape. We intend to do so in the near future. Moreover, the study of pure cembran pine stands will be carried out according to a protocol similar to the one used for the study of mixed stands. Permanent inventory plots could be set up in both types of stands.

The closing of openings by spruce and cembran pine seedlings will require a grid inventory so as to better determine the dynamics of both the closing of present openings and the progression of the timberline. We are considering completing this work with a dendrochronological study, which could provide us with some information decisive to the understanding of the cembran pine stand dynamics. Such a study could also help us to better understand the long-term evolution of forest ecosystems under the influence of environmental changes.

A paleoecological study is under way. It is being carried out by the Vanoise Natural Park. The University of Chambéry has begun a study on the cembran pine cone production and its seed propagation. In addition, they are considering carrying out a historical study of the use of space, using the different cadastres available. They also intend to study the carbon stocking modification in the different soil horizons in the case of an upward progression of the timberline.

Finally, we intend to analyze the possible correlation between the biodiversity indicators and the different structures we have observed.

All these studies should enable us to have a better knowledge of the Tueda cembran forest and of its evolution mechanisms, and they should tell us if maintaining diversity requires some form of management, and, if so, which one.

CONCLUSIONS

We have noted the Tueda cembran pine stand presents very distinct types of structure. In some, cembran pine is predominant, in others spruce is. Some have a sparse canopy, others a very dense one. Regeneration can be either nonexistent or abundant, with a predominance of either cembran pine or spruce. Six stand groups have been determined. What matters to us now is to have a better knowledge of their evolution and dynamism so as to manage them as well as possible. We are considering carrying out some additional studies.

It is likely that cembran pine requires a more energetic form of silviculture than the one we consider today in the lower part of its belt (lower subalpine and upper montane belt), where it is in competition with spruce. The aim of this silviculture is of course to favor cembran pine development, to maintain a structure diversity, and to give it a place of choice, protecting it, among other things, against possible domination by spruce.

In the middle subalpine belt a minimal silviculture, or even no silviculture at all, would be better adapted to these altitudes where the stands are very stable, irregular, and of very slow growth. Other sectors like the station of *Linnaea borealis* would require specific protection.

Practices determined according to the dynamism specific to each ecological system will enable us to enhance the alpine landscapes and to restore their authenticity, while maintaining, if not increasing, their biodiversity.

PLAN 1 2 AXE 1 HORIZONTAL

AXE 2 VERTICAL

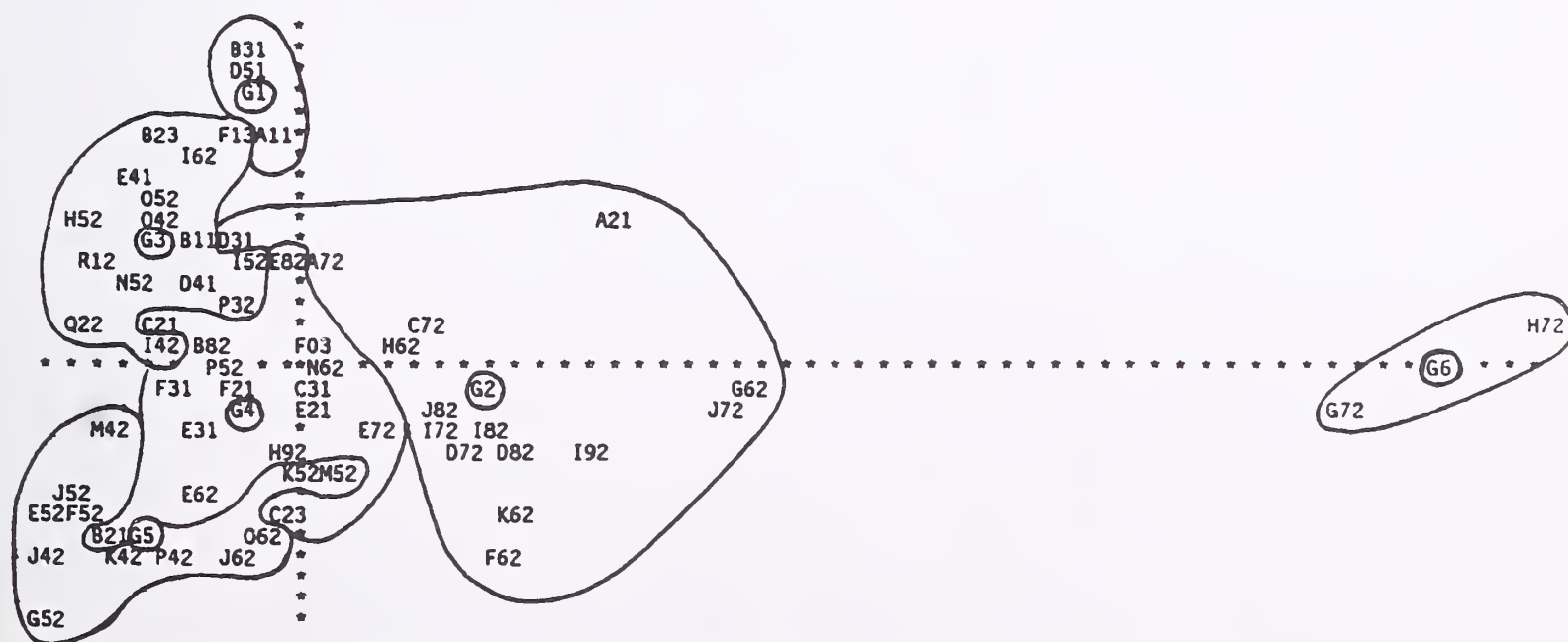


Figure 5—Localization of individuals and groups (Factorial Discriminant Analysis).

REFERENCES

- Bartoli, Ch. 1966. Etudes écologiques sur les associations forestières de la Haute Maurienne - Annales des sciences forestières (Tome XXIII. Fascicule 3. 1966. 321 p.).
- Combes, F. 1986. Le Pin cembro dans les Alpes de Haute Provence (*Pinus cembra* L.). Revue forestière française. N°2: 135-139.
- Contini, L.; Lavarelo, Y. 1982. Le Pin cembro (*Pinus cembra* L.), Répartition, Ecologie, Sylviculture et Production - Institut national de la Recherche agronomique. 197 p.
- Crocq, C. 1990. Le Casse-Noix moucheté (*Nucifraga caryocatactes*). 326 p.
- Del Favero, R.; De Mas, G.; Lasen, C. - Paiero, P. 1985. Il Pino cembro nel veneto. 91 p.
- Fourchy, P. 1968. Notes sur le Pin cembro (*Pinus cembra* L.) dans les Alpes françaises. Revue forestière française. N°2 Février: 77-94.
- Inventaire Forestier National Français. 1986. Résultats du deuxième inventaire forestier. Département de la Savoie. TOME 1. 142 p.
- Inventaire Forestier National Suisse. Résultats du premier inventaire 1982-1986. 375 p. et cartes thématiques.
- Leclerc, D. 1992. Traitements statistiques des données de TUEDA. Office National des Forêts. Section Technique Interrégionale des Alpes du Nord. 43 p.
- Ozenda, P. 1985. La végétation de la chaîne alpine dans l'espace montagnard européen. 344 p.
- Pignol, V. 1992. Procès-verbal d'aménagement de la forêt communale de LES ALLUES. Massif de Tueda. 1992-2002. Office National des Forêts. 63 p.

Forest Management



International Workshop
St. Moritz 1992

SILVICULTURAL TREATMENT AND AVALANCHE PROTECTION OF SWISS STONE PINE FORESTS

Werner Frey

Abstract—Subalpine European larch (*Larix decidua*)-Swiss stone pine (*Pinus cembra*) forests show a natural succession of larch and stone pine that is strongly influenced by natural disasters. Silvicultural treatment has to consider natural tendencies, particularly retaining a permanent amount of larch. On the other hand, stone pine-dominated forests are more efficient for avalanche protection than larch-dominated forests. The application of new results of avalanche research on larch-stone pine forests including their silvicultural treatment is discussed.

This paper gives a short overview on the natural development and regeneration of the subalpine European larch-Swiss stone pine forests in the central European Alps. In these forests, the mutual amount of larch (*Larix decidua* Mill.) and of stone pine (*Pinus cembra* L.) is strongly influenced by natural disasters such as avalanches, snow load, and storms. The ability to protect, especially against avalanches, is different in different types of the larch-stone pine forest. This necessitates different silvicultural treatments.

NATURAL DEVELOPMENT AND REGENERATION

We use the term "European larch-Swiss stone pine forest" (*Larici-Pinetum cembrae*; Ellenberg and Klötzli 1972) for the natural community of these types of forests throughout the central European Alps. Older names refer mostly to *Rhododendron*-rich varieties.

The natural development of the European larch-Swiss stone pine forests is described by Auer (1947), Campell (1955), Ellenberg (1978), Ellenberg and Klötzli (1972), Mayer and Ott (1991), and other authors. The larch-stone pine forests develop only in the more continental climate in the subalpine zone of the Alps. The different stages can be explained by the fact that larch is a pioneer species and stone pine is a climax species.

One main reason for the different behavior of larch and stone pine is the difference in size of seeds: larch seeds are windborne and have a weight of about 0.005 g each; stone pine seeds are heavy (0.25 g each) and dependent on animals for transport. Germination in mineral soil is possible for both species, but there will be far more larch

seeds available in such places, and larch dominates the initial stages. The period of larch domination lasts for about one century. With the gradual building up of a litter layer on the forest floor, regeneration becomes difficult for larch seedlings that cannot reach the mineral soil under the duff layers. In such places, successful regeneration is possible only for seedlings of stone pine. Stone pine needles thicken the duff layer, and finally the larch-stone pine forest turns into a pure stone pine forest. A new initiation of this process is often produced by natural disasters such as avalanches, heavy snow load, and storms that uproot stone pines thus exposing mineral soil.

In the subalpine zone, the growth of stone pine is very slow. Its dominance in the continental Alps is based mainly on four factors: winter frost hardiness, resistance to winter desiccation (Frey 1983), ability to use the short vegetation period, and a quite high shade tolerance. Compared to stone pine, larch finds less optimal growth conditions in the subalpine zone of the central Alps: its growth is well adapted to the short vegetation period but is combined with less winter frost hardiness, less resistance to winter desiccation, and a poor shade tolerance.

If the natural succession is not disturbed by humans or by catastrophic events, these factors usually lead to the development of pure stone pine climax stands.

AVALANCHE PROTECTION

In mountainous regions, forests are most important for avalanche control (to prevent formation of avalanches endangering settlements or traffic routes at the foot of mountain slopes) (Frey and Salm 1990). In the Upper Engadine, as in many other European regions, cultivation of agricultural land in the past resulted in the clearing of sunny slopes. Development of the villages and their increasing dependence on roads induced a need for avalanche protection. Since forests are known to be a good and sustainable protection measure, many areas of afforestation have been established since the 19th century. Figures 1 and 2 show some aspects for the Upper Engadine, Switzerland. Data can be found in Auer (1947), Bundesamt für Forstwesen (1982), and Schlatter (1935).

How does a forest protect areas from avalanches? Some recent results of snow and avalanche research help answer this question (Frey and Salm 1990; Gubler and Rychetnik 1991; Meyer-Grass and Schneebeli 1992). Most of these results originate from spruce and larch stands near timberline in the region of Davos. The effect of stone pine on the formation of snow cover is quite similar to the effect of spruce (Schiechtl 1973).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Werner Frey is Forestry Engineer and Scientist at the Swiss Federal Institute for Snow and Avalanche Research, CH-7260 Davos Weissfluhjoch, Switzerland.

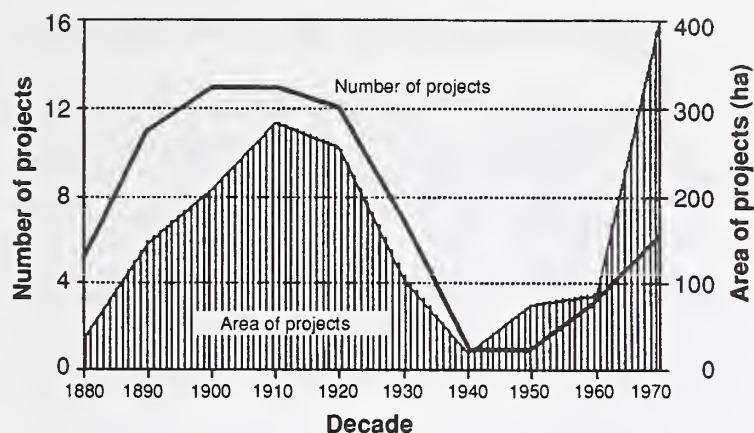


Figure 1—Project area and time of establishment of important afforestation areas to protect villages and main roads: Upper Engadine (see fig. 2).

Snow interception by trees is a very important factor in preventing avalanches. It has two main effects on the formation of extreme avalanches: first, it modifies the distribution and rate of accumulation of new snow during storms; second, between storms it alters the old snow layers including the snow surface.

Radiation also influences strongly the quality of the snowpack in the forest. Incoming shortwave radiation heats needles, branches, and stems. Temperatures rise

above the melting point, and intercepted snow falls into the snowpack. This produces a strong pattern of disturbance and prevents the formation of weak layers in the snowpack that can result in dangerous slab avalanches.

Deciduous larch shows significant differences in snow interception and influence on radiation compared to evergreen spruce and stone pine. In relation to an open field, the incoming shortwave radiation and longwave radiation loss amounts to only 15-30 percent for larch, but up to 90 percent for stone pine. Adding differences in snow interception, mean snow depth reduction is 10-30 percent in open larch stands, and up to 90 percent in dense stone pine stands. Mostly during and after heavy snow storms, stone pine prevents the formation of weak layers in the snowpack more than larch does.

Compared to equivalent conditions in an open field, dry slab avalanches in openings of subalpine forests only start at considerably steeper (5°) inclinations. The thickness of surface slab in forest openings is significantly increased (Meyer-Grass and Schneebeli 1992). Both factors point out the protection ability of subalpine forests.

The structure of subalpine forests is important to avalanche protection. Gubler and Rychetnik (1991) found that extreme dry-slab avalanches may start in openings with downslope lengths of as little as 30 m and widths of 15 m. Smaller avalanches may start in openings with widths of only 10 m (Meyer-Grass and Schneebeli 1992). These facts necessitate small-scale management techniques.

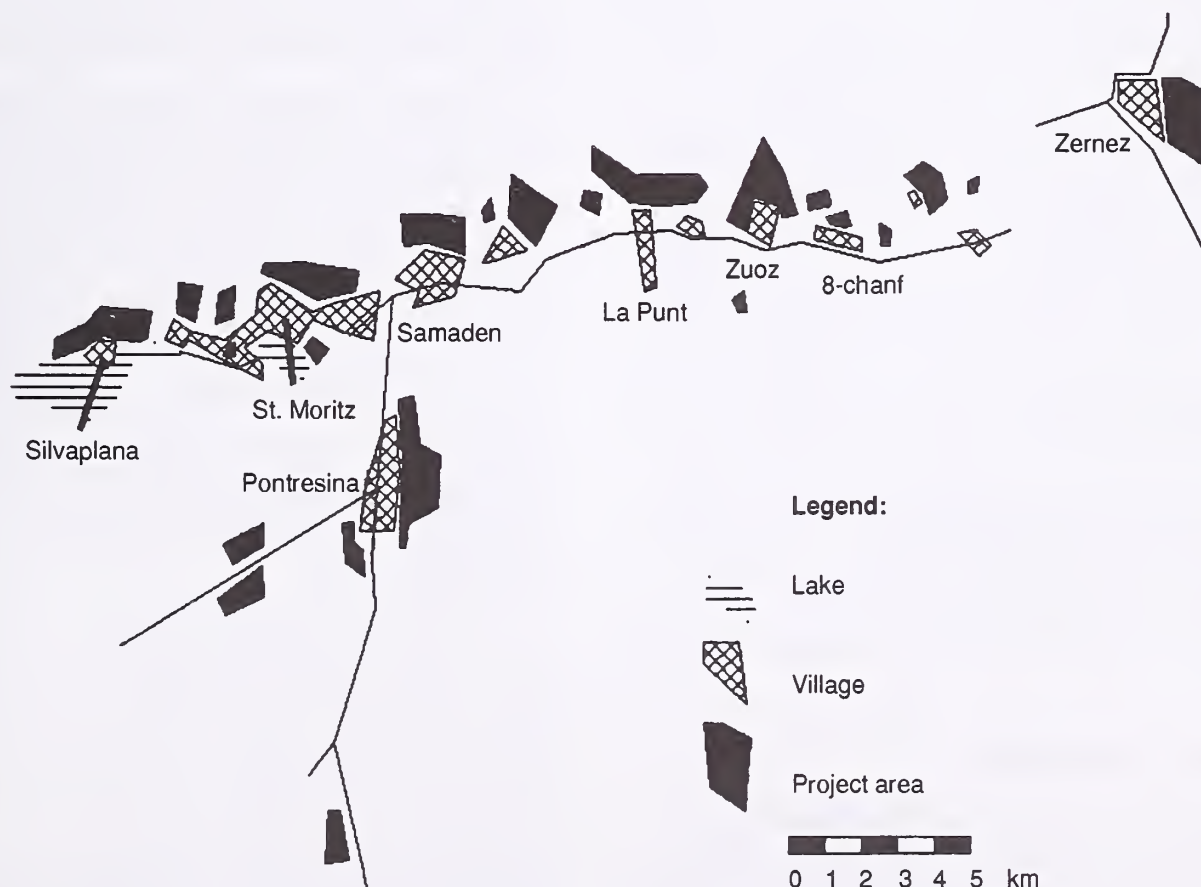


Figure 2—Project areas of afforestation protecting villages and main roads in the Upper Engadine established from about 1860 to 1980. Note that these areas are mostly southern exposed.

The differences between larch-dominated forests and spruce/stone pine-dominated forests in avalanche protection can be summarized: (1) dense stone pine stands, particularly if multilayered, effectively prevent the formation of extreme slab avalanches; (2) open larch stands near timberline do not significantly hinder the formation of extreme avalanches. In addition to these findings of Gubler and Rychetnik (1991), Meyer-Grass and Schneebeil (1992) observed that sufficient dense clustered larch forests give effective protection from the formation of smaller avalanches.

For avalanche protection, the silvicultural goal must be a mosaic of clustered stands, sufficiently dense, multilayered, with mixed species, and uneven-aged. Clusters of different age and, therefore, different protective capability should alternate in space (Gubler and Rychetnik 1991).

PROTECTION FROM EROSION

It is difficult to judge generally the erosion protection value between different tree species and forest types. Important factors such as geology and precipitation change in space, and soil and topography may change on an even smaller scale. However, for protection from erosion Mayer and Ott (1991) characterize the species of larch-stone pine forests as follows: stone pine is able to retain much more precipitation than larch and stemflow is reduced by the coarse bark of both larch and stone pine. In rocky soils stone pine is deeper rooting than larch. The silvicultural goal, therefore, is quite similar to the goal in avalanche-protection forests: a natural mixture of larch and stone pine, sufficiently dense, multilayered, and uneven-aged.

SILVICULTURAL TREATMENTS

In larch-stone pine forests the full succession from pioneer stands rich in larch to mature stone pine stands takes more than 400 years (Mayer and Ott 1991). Sufficient avalanche and erosion protection can be guaranteed only by a small-scale mosaic of multilayered and clustered forest types. Both natural development and the objective of protection eliminate all large-scale silvicultural treatment methods.

Different silvicultural treatments are used for different types of forest utilization:

1. Grazing woodland or forested recreation areas on gentle slopes with little need for protection.
2. Forests on gentle or steeper slopes used for wood production but also for protection.
3. Avalanche- and erosion-protection forests mostly on steep slopes.

Small-Scale Methods

Before talking about silvicultural methods used in the different utilization types, we have to introduce some small-scale silvicultural treatment methods that are generally used in the European Alps. Details can be found in the publications of Auer (1947), Aulitzky and Turner (1982), Bischoff (1987), Campell (1955), Mayer and Ott

(1991), Pitterle (1988), Piussi and Schneider (1985), and Trepp (1981).

Selection Method (single-tree selection method; German term "Einzelplenterung")—The individual harvesting area of this method is very small. Harvesting is realized by felling single selected trees from different stories, retaining and creating favorable conditions for regeneration at the same time. Forests managed by this method are multilayered and clustered and show a mixture of all tree ages over very small areas. This method as used in the past showed a strong tendency to eliminate larch in the larch-stone pine forest.

Cluster Selection Method (small-scale, group-selection method; German terms "Gebirgsplenterung" or "Gruppenplenterung")—The individual harvesting area is quite small. In subalpine forests, trees usually grow in an arrangement of small clusters in which trees mutually protect each other (Schönenberger and others 1990). These clusters are now considered as individual trees; the group-selection method harvesting whole tree clusters is aiming at the same goal as the single-tree selection method.

Group Selection Method (German term: "Femelschlag")—Harvesting areas are bigger and may vary from one-third to several hectares. The local distribution of successional stages and the variability of sites define the harvesting area. Regeneration nuclei and logging aspects have to be taken into consideration.

Use of Methods

These silvicultural methods in the larch-stone pine forest are applied in three types of areas:

1. Grazing woodland or forested recreation areas on gentle slopes. The aim is an open structure with a good portion of larch. These forests are open to warmth and light. Selection harvesting of mature trees combined with measures promoting natural regeneration or planting is best suited to the management objectives. Young trees have to be protected against deer and cattle if necessary.
2. Forests on gentle or steeper slopes grown primarily for wood production. The natural succession is leading to quite pure stone pine forests and can be accelerated using the single-tree selection method. A higher amount of larch can be obtained using the group-selection method or the cluster-selection method, if necessary sustained by soil stripping (scarification) to prepare a good germination bed for larch.
3. Avalanche and erosion protection forests, mostly on steep slopes. The stability of these forests in time and space is dependent on a sufficient proportion of larch to prevent the disintegration of overmature stands composed purely of stone pine. On the other hand, stone pine is more effective in avalanche and erosion protection. A permanent protection effect needs sufficient, well-dispersed regeneration. In potential avalanche starting zones, openings should not exceed downslope lengths of 30 m and widths of 15 m. The cluster-selection method best fits these management objectives.

SUMMARY AND CONCLUSIONS

Natural succession in larch-stone pine forests starts with a high amount of larch germinating and growing well on mineral soil. Mature larch stands produce a relatively shaded forest floor and a building up of a duff layer covered by a needle layer. These conditions favor germination and growth of stone pine. Mature stands consist predominantly of stone pine. Natural succession is initiated by disasters such as avalanches, heavy snow load, or storms. The succession period will last for more than 400 years.

The silvicultural goal for good avalanche and erosion protection must be a natural mosaic of larch and stone pine stands in a clustered structure, sufficiently dense, multilayered, and uneven-aged.

Experience has shown that the best silvicultural methods for wood production are the group-selection or the cluster-selection methods that allow the favoring of either larch or stone pine according to management needs. The most suitable method for protection purposes is the cluster-selection method.

ACKNOWLEDGMENTS

Thanks to Ian McCracken, Walter Schönenberger, Martin Meyer-Grass, Walter Ammann, and Reinhard Lässig, who reviewed the manuscript critically.

REFERENCES

- Auer, C. 1947. Untersuchungen über die natürliche Verjüngung der Lärche im Arven-Lärchenwald des Oberengadins. Eidg. Anst. forstl. Versuchswes., Mitt. 25(1): 7-140.
- Aulitzky, H.; Turner, H. 1982. Bioklimatische Grundlagen einer standortgemässen Bewirtschaftung des subalpinen Lärchen-Zirbenwaldes. Eidg. Anst. forstl. Versuchswes., Mitt. 58(4): 325-580.
- Bischoff, N. 1987. Pflege des Gebirgswaldes. Leitfaden für die Begründung und forstliche Nutzung von Gebirgswäldern. Bern, Bundesamt für Forstwesen und Landschaftsschutz. 379 p.
- Bundesamt für Forstwesen. 1982. Lawinenverbau- und Aufforstungskataster. Bern.
- Campell, E. 1955. Der Lärchen-Arvenwald (Alpenrosen-Heidelberggesellschaft, Rhodoreto-Vaccinietum). In: Ertragreiche Nadelwaldgesellschaften im Gebiete der schweizerischen Alpen... von E. Campell, R. Kuoch, F. Richard, W. Trepp. Bündnerwald, Beiheft 5: 14-26.
- Ellenberg, H. 1978. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Verlag Eugen Ulmer, Stuttgart. 982 p.
- Ellenberg, H.; Klötzli, F. 1972. Waldgesellschaften und Waldstandorte in der Schweiz. Eidg. Anst. forstl. Versuchswes., Mitt. 48(4): 589-929.
- Frey, W. 1983. The influence of snow on growth and survival of planted trees. Arctic and Alpine Research. 15(2): 241-251.
- Frey, W.; Salm, B. 1990. Snow properties and movements in forests of different climatic regions. In: Proc. XIX IUFRO World Congress, Montreal, Canada, Div. 1, Vol. 1: 328-339.
- Gubler, H.; Rychetnik, J. 1991. Effects of forests near timberline in avalanche formation. In: Bergmann, H.; Lang, H.; Frey, W.; Issler, D.; Salm, B., eds. Snow, hydrology and forests in high alpine areas. IAHS Publ. 202: 19-38.
- Mayer, H.; Ott, E. 1991. Gebirgswaldbau - Schutzwaldpflege: Ein waldbaulicher Beitrag zur Landschaftsökologie und zum Umweltschutz. 2. Auflage. Gustav Fischer Verlag, Stuttgart. 587 p.
- Meyer-Grass, M.; Schneebeli, M. 1992. Die Abhängigkeit der Waldlawinen von Standorts-, Bestandes- und Schneeverhältnissen. In: Schutz des Lebensraumes vor Hochwasser, Muren und Lawinen. Interprävent, Bern. 2: 443-445.
- Pitterle, A. 1988. Waldbauliche Analyse und Behandlungsmassnahmen von anthropogen beeinflussten subalpinen Fichten- sowie Lärchen-Zirbenwäldern im Villgratental/Osttirol. Diss. Univ. Bodenkultur, Wien. 225 p.
- Piussi, P.; Schneider, A. 1985. Die obere Wald- und Baumgrenze im Pfitschtal (Südtirol). [Upper forest limits and treelines in the Pfitschtal, South Tyrol]. Cbl. ges. Forstw. 102(4): 234-246.
- Schiechl, H. M. 1973. Wiederbewaldung von Extremstandorten - Grundlagen und Voraussetzungen in den Hochlagen und auf Rohböden. Allgem. Forstztg., Wien. 84(10): 243-245.
- Schlatter, A. J. 1935. Die Aufforstungen und Verbauungen des Oberengadins in den Jahren 1875-1934. Schweiz. Z. Forstwes. 86.
- Schönenberger, W.; Frey, W.; Leuenberger, F. 1990. Ökologie und Technik der Aufforstung im Gebirge - Anregungen für die Praxis. Eidg. Anst. forstl. Versuchswes., Ber. 325. 58 p.
- Trepp, W. 1981. Das Besondere des Plenterns im Gebirgswald. Schweiz. Z. Forstw. 132(10): 823-846.

IMPORTANCE AND SILVICULTURAL TREATMENT OF STONE PINE IN THE UPPER ENGADINE (GRISONS)

Riet Gordon

Abstract—The European larch (*Larix decidua*)-Swiss stone pine (*Pinus cembra*) forests of Celerina have been affected by humans for centuries. Today's demands on the forest have an important influence on the silvicultural treatment of these forests. The stone pine, as the naturally best-adapted tree species in Celerina, suffers from the consequences of public demands. The selective cutting of stone pine often appears necessary to promote the Scots pine and larch as the most important tree species for conservation and recreation functions. Nevertheless, in the future stone pine will continue to be the most important tree species in the forests of the Upper Engadine.

Most of the alpine forests have been affected by humans for centuries. The European larch (*Larix decidua*)-Swiss stone pine (*Pinus cembra*) forest in the Upper Engadine is no exception. Human influence is apparent in the forest structure and species composition (Ganzoni 1911). In recent times, the demands on the forest have changed. Thus forest management and treatment have also changed.

This paper discusses the management and treatment of stone pine forests in an area often used by the public. Three examples from the forest enterprise in Celerina are presented.

HISTORY OF CELERINA'S FORESTS

Until the end of last century, the forests in Celerina were used for wood production for local purposes and for grazing indigenous cattle and enormous herds of sheep from Italy. These sheep used to spend the summer in the Upper Engadine (Schlatter 1935). In addition, forest litter was used as bedding in the cattle stables, and in times of famine stone pine seeds even served as an additional source of food for the local people.

The village constitution includes forest laws dating back to 1699 (Ganzoni 1982). The evolution of these laws demonstrates the importance of the forests to the village community. Only the village community as a whole had the right to use the forest, not the individual inhabitant. To enforce these laws, the village employed forest guards. The wood was normally used by the village community, and only in special cases was it sold. The inhabitants of the village were entitled to a limited amount of building wood and firewood, but only for their own personal use. They were also allowed to collect litter, peat, or stone pine cones.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Riet Gordon is Forestry Engineer and Scientist, Swiss Federal Institute of Technology, Department of Forestry, CH-8092 Zurich, Switzerland.

During the 17th and 18th centuries, the exploitation of some forests in Celerina was prohibited. The preserved forests were not "protection forests" as in many places in the Alps; they were probably forests that had been over used. The ban on exploitation can be considered as the beginning of forest management.

With the exception of the preserved forests, all forests had been intensively pastured until the end of the 19th century. The first regulations concerning pasturing date from 1860. From then on, grazing in the forests of Celerina decreased, except during times of economic crises when the forests were intensively pastured again.

At the beginning of the present century, the forests of Celerina became important as a recreation area for the local people and tourists. During the first decade, the forests were frequented mostly in summer by a few tourists. Today, they are frequented by thousands of people for hiking, riding bicycles, skiing, and horseback riding throughout the year. The first forest management plan in 1888 already included some notes concerning the recreation function of the forest. It was proposed to establish more and better trails and to keep them clean of branches and fallen trees. This illustrates the importance of the forests to tourism as early as the beginning of the 20th century.

In the Swiss lowland forests many plants and animals became extinct (Schweiz Bund f. Naturschutz 1992). In contrast to the lowland forests, the mountain forests are still quite natural. Therefore they are increasingly important for nature and landscape conservation. In Celerina, conservation in the forest gained some importance when the marvelous upland moors in the "Stazerwald" were put under protection in 1956.

How does this evolution influence the occurrence and the treatment of the stone pine? Larch was the most important species in the forests of Celerina until 1970, especially on the south-facing slopes. Larch produces very good and durable wood for construction. It was especially used for houses and barns but also for artificial barriers to prevent floods and soil erosion, for water pipes, etc. The open larch forests were suitable for grazing by cattle and sheep and litter production for the farmers.

For a long time stone pine was used only for firewood or as construction wood of minor quality. In the dark stone pine forests the pasturage did not have a very high production level and litter production was lower than in larch forests. Therefore, the management gave stone pine a low priority compared to larch.

The situation today has changed. The forest enterprise is based financially on the valuable stone pine wood. Its value is nearly four times greater than that of spruce or larch wood.

FOREST MANAGEMENT

Since 1888, the forest of Celerina has been cultivated on the basis of a management plan. The objective of this management has always been the quantitative preservation of the forest. At the end of the 19th century, most of the mountain forests were heavily damaged by grazing, wood over-exploitation, avalanches, and erosion. The management was mainly focused on wood production. Through periodic inventories, first by the full enumeration method and later by sample plots, the state and the development of the growing stock, stem count distribution, species composition, and growth increment have been determined. The result of the planning process was the prescribed yield, which was compulsory for 10-20 years.

A kind of silvicultural planning already existed in the first management plan. It was based mainly on natural sites. The functions of the forest were not yet considered.

The forest management was performed by the State Forest Service and not by the forest owner.

Management in the Future

In the beginning of this century, quantitative forest conservation was the main goal of forest policy, a goal that has been achieved (Bachmann 1991). Today, qualitative forest conservation is the main aim of forest policy. The forest management has to follow this new objective to be credible for the Forest Service, the forest owner, and the general public. What are the needs for the future?

Elaborating the general aims of the forest enterprise is not an exclusive affair of the State Forest Service, because the interest of the public in the forest is becoming increasingly important. The forest owner and especially the public have to be integrated in the target process, to consider their demands for the forests.

The Forest Service is no longer the only institution where decisions concerning the forests are made. More and more it takes charge of consultative and coordinative functions. The decisions are made in a democratic process open to the general public. This does not mean that every demand of the public on the forests has to be accepted and realized. The qualitative preservation of the forest is still the main aim and, of course, it has priority in case of conflicts between the demands and forest preservation. The results of the target process are presented and illustrated on a forest function map (fig. 1).

Information Needs

Management and silviculture treatment have to be harmonized with the forest functions. The need for information is related to the forest functions. For the mountain forest the following information is of primary importance:

1. Stand description, which consists of the development stage, canopy closure, structure, and species composition.
2. Stability, which shows the ability of a forest stand to remain constant or to persist in the face of disturbance factors such as wind, snow, avalanches, and soil erosion. Stability is described by the following main features: regeneration, structure, and density of the stand, canopy size, root anchorage, and damage to the single trees (Ott 1988).

3. The ability of a forest stand to continuously provide all the demands allocated to it by main function suitability.

The inventory methods have to be adapted to this need for information. The present sample inventory is therefore replaced or enhanced by a stand-based inventory.

Some examples of the management plan of Celerina illustrate the silvicultural consequences due to forest functions.

PROTECTION FORESTS

The forests of Celerina have a relatively small direct protection function compared to other mountain forests. Nevertheless, some forests with a particular protection function have been determined. For these forests the following silvicultural objectives have been fixed:

1. A small-scale mosaic of all size and age classes (cluster selection forest).
2. At least 60 percent stone pine, less than 40 percent larch.
3. Stable forest communities.

This aim can be achieved only by regular silvicultural treatment. Stone pines must be promoted. Damage to the remaining stand due to logging or other influences must be avoided. Therefore, a minimal basic network of truck roads is needed in some places to enable logging with mobile cable cranes. Other forest functions have to be subordinated to the protective function of the forest. To solve conflicts in the protection forests in Celerina the following general measures are necessary:

1. Preventing deer damage to trees by reducing the number of deer.
2. Excluding pasture from the protection forest.
3. Regulating "wild" skiing outside the official skiing runs.

More information about the avalanche protection function of the forest and silvicultural treatment of European larch-Swiss stone pine forests was presented by Frey (these proceedings).

RECREATION FORESTS

Recreation is of great importance in the forests of Celerina. Recreation forests should have a diversified structure, density, and species composition. Existing clearings have to be preserved as well as special trees, particular sites, etc. The visual image of the recreational forest in Celerina is more important than its wood production.

Recreation function requires the promotion of larch and Scots pine (*Pinus sylvestris*) instead of stone pines. Larch and Scots pine are pioneer trees and therefore are difficult to regenerate in closed forests. Special regeneration techniques such as larger regeneration cuts than usual and soil scrapes have to be applied. A further measure in recreation forests is to cut old trees later than proposed by yield models.

Recreation forests need a special infrastructure. In summer, the forests of Celerina must have trails, horse trails, bicycle paths, picnic and fire places, fitness courses, and an information trail explaining the forests as an ecosystem. In winter, walking paths, cross-country skiing

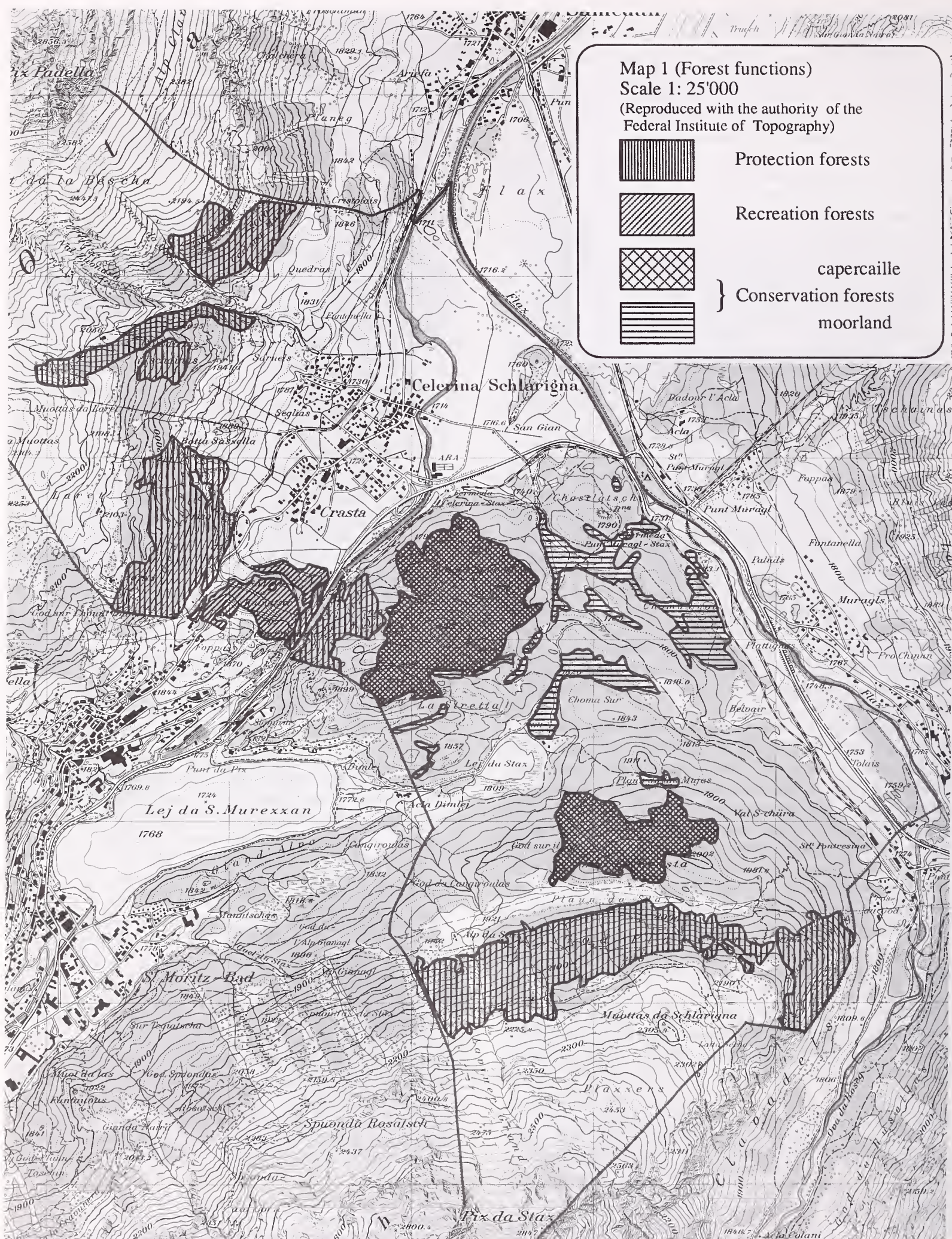


Figure 1—Forest functions in the Celerina area of the Upper Engadine in Switzerland.

Table 1—The different functions and their consequences for the silvicultural treatment

Function	Stone pine	Larch	Structure	Density	Yield	Remarks
	-----Percent-----				Age	
Multifunction	60	40	Clustered	Normal	200	
Protection	>60	<40	Clustered	Closed	<200	No damage, no big openings
Recreation	60	40	Clustered	Normal	>200	Infrastructure
Conservation (capercaillie)	>60	40	Clustered	Normal Open	>200	Old trees, clearings, any accessibility, silence
Pasture	20	>60		Open	>200	
Wood production	>60	<40	Clustered	Normal	200	Accessibility

tracks, and downhill ski runs have to be maintained. The Forest Service is not the only authority responsible for the infrastructure, but nevertheless it has an important coordinating function.

The recreation function involves some conflicts especially with regard to nature conservation for species such as a large grouse in the area, the capercaillie (*Tetrao urogallus*), hunters (disturbance of deer), and forest accessibility. These conflicts have been smoothed by separating the different demands on the forest in time and space.

CONSERVATION FORESTS

For nature conservation two factors are important: protection of moorlands (bogs) and the habitat of the capercaillie. The preservation of moorland demands that, due to natural regeneration of young stone pines and mountain pines (*Pinus montana*), young trees have to be removed continuously. Other silvicultural or technical measures are neither necessary nor desired. Bog areas should be kept free of paths, cross-country tracks, and drainage ditches. There are only a few areas left today that are not influenced by these impacts, because the most important cross-country track in the area goes through the most beautiful and largest bog.

The preservation of the "Stazerwald" as an important habitat for capercaillies is considered the second essential objective of conservation. Therefore the forester has to favor Scots pine, a large number of old trees, and sufficient open areas within the forest.

The preservation of Scots pine is quite difficult. Natural succession goes from Scots pine to stone pine. This development has to be stopped by favoring the natural regeneration of Scots pine through exposing the mineral soil. Often this measure is not sufficient to enhance Scots pine regeneration, and additional planting is necessary.

Besides these silvicultural measures, other precautions are necessary to preserve the capercaillie in the "Stazerwald." During mating and breeding time and in winter, the territory of the capercaillie should not be disturbed by humans. For this reason, silvicultural work should be delayed until after mid-July. Before that not even tourists should cross these habitats. Therefore, some walking

paths and cross-country tracks have to be closed to the public. Trespassing on the forests outside walking paths is restrained until the middle of July.

CONCLUSIONS

The different demands of the public on the forests have to be taken into consideration during planning. Silvicultural objectives and measures, control, and need for information (Informationsbedarf) depend on the forest functions.

Considering the public demands on the forest, the Swiss Forest Service nevertheless uses multifunctional forest management. However, many specific demands, well defined in time and space, can only be achieved if the treatment is adapted to these special objectives. It is not possible to achieve these objectives only by wood production.

The consequences for silvicultural treatment of the forest of Celerina are shown in table 1.

The stone pine, as the naturally best-adapted tree species in Celerina, is most affected by public demands because it is mainly stone pine that has to be "cut back." Nevertheless, in the future stone pine will continue to be the most important tree species in the forests of the Upper Engadine.

REFERENCES

- Bachmann, P. 1990. Forsteinrichtung und Walderhaltung. Schweiz. Z. Forstwes. 141(6): 415-430.
- Ganzoni, G. P. 1982. Monografia da Schlarigna. Uniu dals Grischs, Schlarigna.
- Ganzoni, Z. 1911. Die Waldungen des Oberengadins. Schweiz. Z. Forstwes. 62: 40-44, 77-81.
- Ott, E.; Schoenbaechler, D. 1988. Stabilitätsbeurteilung im Gebirgswald als Voraussetzung fuer die Schutzwald Ueberwachung und Pflege Schweiz. Z. Forstwes. 137(1986): 725-738.
- Schlatter, A. J. 1935. Die Auforstungen und Verbauungen des Oberengadins in den Jahren 1875-1934. Schweiz. Z. Forstwes. 86(1935)9: 309-328.
- Schweizer Bund f. Naturschutz. 1992. Naturwald. Sonderheft Nr. 3, Basel.

CULTIVATION OF CEMBRAN PINE PLANTS FOR HIGH-ELEVATION AFFORESTATIONS

Jörg Heumader

Abstract—In this paper a special “biological” method of cultivating cembran pine (*Pinus cembra*) plants for high-elevation afforestation is described. This method produces fully mycorrhized transplants and pot plants, which have proved to be well adapted to the harsh environment of subalpine and timberline areas in the Inner Alps of Austria.

The Alps are probably the most intensively settled and used high-mountain range in the world. Originally, the economic base of the settlements in the Alps was livestock, and a special ranching and grazing system was developed. Large areas in the timberline region were deforested for livestock grazing in summer and for producing hay for the winter time.

Natural hazards are “normal” phenomena in high-mountain ranges—with and without anthropogenic influences. On some sites, deforestation by humans had negative effects. Deforesting unstable mountain sides or steep slopes sometimes led to and sometimes increased torrent, avalanche, or rockfall disasters.

One of the tasks of the Austrian Federal Service for Torrent and Avalanche Control, therefore, is planning and conducting high-elevation afforestation in subalpine areas deforested long ago (fig. 1). High-elevation afforestation in the Tyrolean Alps got a strong impetus from the avalanche catastrophe of 1951. Many disaster-prevention projects with integrated control measures were planned, and many plants adapted to timberline conditions were needed, especially cembran pine (*Pinus cembra*).

Cembran pine plants were hard to get and not much was known about their cultivation at that time. Therefore, the Federal Service for Torrent and Avalanche Control in Tyrol not only started a research program on subalpine forests but also founded in 1953 the tree nursery “Klausboden” for the production of native subalpine tree species.

CULTIVATION PRINCIPLES

The cultivation method for cembran pine plants was to be developed to a high standard in this nursery in close cooperation with the Federal Forest Research Institute (Heumader and Gobl 1990; Leys 1970).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Jörg Heumader is Graduated Engineer of Forestry, Federal Service for Torrent and Avalanche Control, Langgasse 88, A-6460 Imst, Tirol, Austria.

The aim from the beginning was the production of plants of high quality and special fitness for subalpine conditions. Research had shown that mycorrhizae are essential for the growth and survival of cembran pine plants (fig. 2), because unmycorrhized plants are not able to get enough nutrients from the thick raw-humus layers in subalpine areas (Gobl 1965).

To produce vital and mycorrhized plants (fig. 3), a special treatment of soil in the nursery and a biological cultivation method were developed with the following characteristics:

- Mycorrhizae inoculation of seed and transplant beds.
- Enrichment of soil by compost and peat to obtain best soil conditions for mycorrhizae growth with pH values between 6.0 and 6.5.
- Green manuring instead of chemical fertilizers, which means that every fourth year each bed is planted with a special mixture of annual plants with a high percentage of legumes for soil regeneration (Czell and Redlich 1966).
- No use of herbicides; weeding is done only hand.

MYCORRHIZAE INOCULATION

For the production of mycorrhized plants, special techniques had to be developed (Gobl 1979; Moser 1958, 1959).



Figure 1—High-elevation reforestation in the Tyrolean Alps with cembran pine and larch (*Larix decidua*) on a mountain side deforested for livestock grazing more than 1,000 years ago.

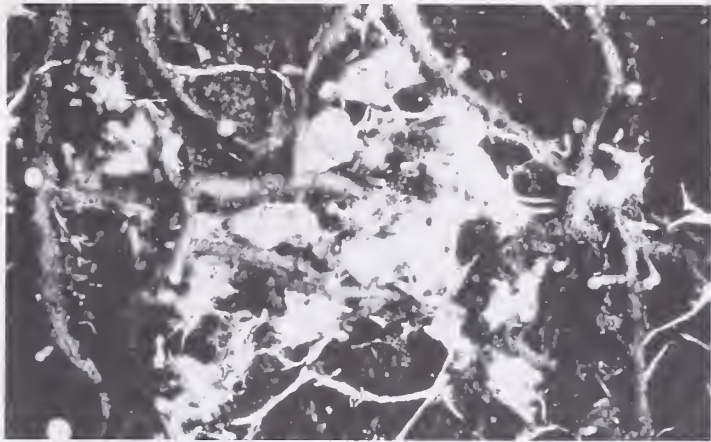


Figure 2—Fine roots of a cembran pine plant with fully developed mycorrhizae.

The selection of suitable fungi was based on investigations in cembran pine forests, especially on sites with good natural regeneration. The two species *Suillus placidus* and *Suillus plorans* were found to be best of all mycorrhizal fungi growing in timberline areas. On



Figure 3—Two cembran pine pot plants of the same age. The better condition and growth of the mycorrhized plant on the left is clearly seen.

natural sites cembran pine mycorrhizae prefer the raw-humus layers of podzolic soils; corresponding to this, peat was found to have the best mycelium growth and therefore was used for cultivation and production of mycorrhizae.

Analyses of sterilized peat, on one hand, and of peat inoculated with mycelium, on the other, have shown that fungi of the species *Suillus* are able to break up the nutrients nitrogen (N) and potassium (K) (table 1).

For mycorrhizae inoculation, peat interlaced with mycelium was mixed with the topsoil of seed and transplant beds in the nursery for many years. Cultivation of cembran pine plants since 1957 has resulted in nursery soil that is now full of mycelium, and therefore inoculation has not been necessary for many years.

CULTIVATION OF SEEDLINGS

Cembran pine seeds are wintered outdoors in thin, alternate layers of seeds and sand inside wooden boxes that are sheltered with wire nets to exclude mice. In this way they can be put into the seedbeds in spring without stratification. The seeds are lying close together and are covered with thin layers of compost and peat. The seedbeds must be shadowed and sheltered against mice and especially nutcrackers, which sometimes are a great problem.

Because of embryo dormancy, 30 to 50 percent of seeds will not germinate in the first year, but will in the following year (fig. 4). Normally, cembran pine seeds have a germination rate of about 60 to 70 percent; this means that 1,800 to 2,000 seedlings per square meter occupy the seedbed by the end of the second year.

TRANSPLANTING

After 3 years, the seedlings, now 2 or 3 years old, are transplanted in rows; in the transplant beds there are about 120 plants per square meter. The best times for transplanting cembran pine seedlings are spring or summer. Transplanting can also be done in autumn, but this can cause frost-heaving problems with insufficiently rooted transplants.

Barerooted transplants are 4 or 5 years old (fig. 5) when used for afforestation, which is done in spring or autumn. Afforestation done in the spring shows better results and less transplant loss than in autumn.

POT-PLANT PRODUCTION

In recent years our tree nursery also produces pot plants. These are cultivated in pots made of pressed peat,

Table 1—Analyzed values of the nutrients N and K of sterilized peat, inoculated by mycelium of *Suillus placidus* after different growth periods

Mycelium growth	NO ₃ - N	NH ₄ - N	NH ₄ - N	ALE	Total
				K ₂ O	K ₂ O
--- mg/100 g ---			Percent	mg/100 g	Percent
Without mycelium	0.95	27	0.18	8	0.01
0-4 weeks	1.47	37	.28	12	.01
5-8 weeks	1.40	68	.34	37	.05



Figure 4—Cembra pine seedlings of two different seed provenances at the beginning of the second year's growing season showing different percentages of dormancy.



Figure 5—Transplants of cembra pine, 5 and 4 years old. At this size they are fit for outplanting. A speciality of the "biological cultivation method" in the tree nursery "Klausboden" is the use of green-manuring plants instead of chemical fertilizers for soil regeneration. This can be seen in the right half of the photo.



Figure 6—High-elevation afforestation with cembra pine and larch for protection of the road crossing the Arlberg Pass between Tyrol and Vorarlberg. Note the steel snow bridges in the background used for stabilizing the snow pack.

which can be pierced by the roots and will rot in a few years. Cembra pine seedlings can be transplanted into these pots in spring and in summer. They are ready for afforestation after 2 or 3 months when their roots are beginning to pierce the pots. Tests have shown that a mixture of 90 percent peat and 10 percent bruised grape seeds is best for mycorrhizae growth in these pots.

FINAL REMARKS

The tree nursery "Klausboden" produces about 60,000 transplants, 100,000 seedlings, and 40,000 pot plants of the stone-pine species cembra pine each year on a bed area of 0.54 hectares. For more than 30 years these plants have proved to be well adapted to the harsh environment of subalpine and timberline areas in the Inner Alps of Austria (fig. 6).

Research work, especially on cembra pine mycorrhizae, has been an important part of the research program

on subalpine forests. This research started in Austria after the avalanche catastrophe of 1951, and it is still going on. Very little is known about the coevolution of mycorrhizal fungi and the other subalpine stone-pine species in Asia and North America.

Because we can be sure that mycorrhizae are essential for the growth and survival of all timberline tree species, it is very important that intensive research be started all over the world on these interrelations.

ACKNOWLEDGMENTS

The author, responsible for running the tree nursery "Klausboden," gives special thanks to Dr. F. Gobl, mycorrhizae specialist, for her cooperation and very helpful ideas concerning the nursery and this paper.

REFERENCES

- Czell, A.; Redlich, G. C. 1966. Die Beeinflussung des Gebrauchswertes von Junglarchen durch kombinierte Wurzel-Grundung (KWGD). Centralblatt fur das gesamte Forstwesen, 83., 2, Osterr. Agrarverlag, Wien: 65-84.
- Gobl, F. 1965. Die Zirbenmykorrhiza im subalpinen Aufforstungsgebiet. Centralblatt fur das gesamte Forstwesen, 82, Osterr. Agrarverlag, Wien: 89-100.
- Gobl, F. 1979. Erfahrung bei der Anwendung von Mykorrhiza-Impfmaterial (.Zirbe). Centralblatt fur das gesamte Forstwesen, 96.1, Osterr. Agrarverlag, Wien: 30-43.
- Heumader, J.; Gobl, F. 1990. Der Forstgarten "Klausboden". Biologische Anzucht von Pflanzen fur Hochlagen seit mehr als 35 Jahren. Wildbach-und Lawinenverbau, Zeitschrift des Vereins der Diplomingenieure der Wildbach-und Lawinenverbauung Osterreichs, Salzburg 54, 113: 85-106.
- Leys, E. 1970. Erfolgreiche Zirbenanzucht. Gebietsbauleitung Oberes Inntal, Imst. 8 p. Unpublished manuscript.
- Moser, M. 1958. Die kunstliche Mykorrhizaimpfung von Forstpflanzen, II. Die Torfstreukultur. Forstwissenschaftl. Centralblatt, 77, Osterr. Agrarverlag, Wien: 273-278.
- Moser, M. 1959. Die kunstliche Mykorrhizaimpfung von Forstpflanzen. III. Die Impfmethode. Forstwissenschaftl. Centralblatt, 78, Osterr. Agrarverlag, Wien: 193-202.

WHITEBARK PINE CONSERVATION IN NORTH AMERICAN NATIONAL PARKS

Katherine C. Kendall

Abstract—Whitebark pine (*Pinus albicaulis*) is a prominent component of high-elevation forests in National Parks in the Western United States and Canada. Park management attempts to conserve genetic integrity and allow natural processes to occur unimpeded in these communities. However, whitebark pine forests are threatened by introduced disease and fire suppression in many areas. Retention of fire-dependent, mixed-species whitebark pine communities will require aggressive programs to introduce fire, or mimic its effects. Emerging efforts to develop blister rust-resistant whitebark pine raise questions about when and to what extent it is appropriate to alter park genetic stock. Precedents set by related cases and Park Service policy guiding genetic resource protection and native plant restoration are summarized. A survey of the status of whitebark pine throughout its range and studies to establish genetic and adaptive variation are most needed. For populations at risk, seed bank collections are urged. Trade-offs of various whitebark pine management alternatives are evaluated.

Forestry Canada and USDA Forest Service personnel manage the bulk of whitebark pine forests. Their nonwilderness lands are managed for multiple use, and a broader range of activities are allowed in their jurisdictions than in National Parks. Because of this, National Parks and wilderness areas serve as benchmarks or experimental controls for national and private forests and lands managed by other agencies for a variety of purposes. Management intervention in National Parks, however, may be appropriate when park resources are changed by human activities.

MANAGEMENT CHALLENGES

Whitebark pine is in jeopardy in many areas from introduced disease and fire suppression. The most serious

Whitebark pine (*Pinus albicaulis*) is a component of high-elevation forests in 15 National Park areas in the Western United States and Canada (fig. 1). Its impact can be found at landscape, community, and species scales. Whitebark pine stands influence snow accumulation and retention, thus affecting hydrological characteristics in the drainages where they occur. As a pioneer at harsh, exposed sites, whitebark pine modifies the microclimate and allows other vegetation such as subalpine fir (*Abies lasiocarpa*) to establish and persist (Habeck 1969). A variety of wildlife, including the threatened grizzly bear (*Ursus arctos*), rely on whitebark pine communities for food and shelter (Hutchins and Lanner 1982; Kendall 1983; Mattson and Reinhart, these proceedings; Tomback 1978).

United States and Canadian National Park policy is to preserve natural ecological and evolutionary processes in their natural areas. Management of individual species such as whitebark pine is typically limited to inventory and monitoring the status of the species. Under current U.S. National Park Service (NPS) management philosophy, changes caused by natural events such as native insect outbreaks or native diseases are not normally interfered with. Practices to increase seed production, artificially reforest naturally disturbed stands, or other management intervention generally are not appropriate.

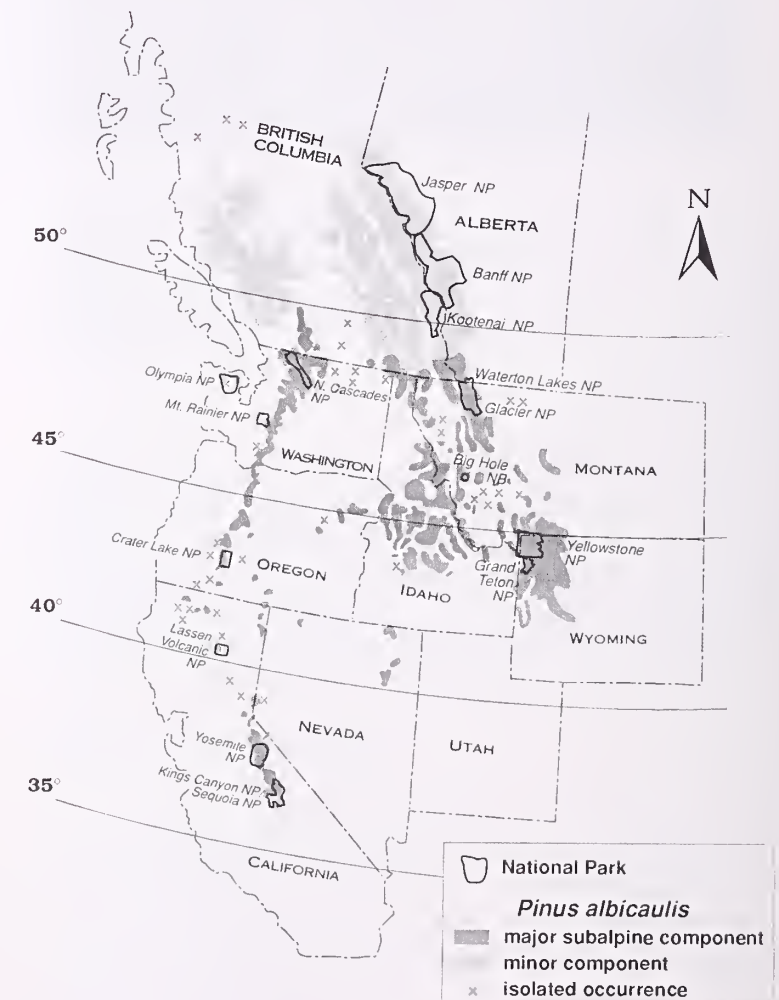


Figure 1—Whitebark pine occurrence in western Canadian and U.S. National Park areas. Distribution data are based on Arno and Hoff (1986) and Ogilvie (1990).

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Katherine C. Kendall is Research Ecologist at Glacier National Park, Science Center, West Glacier, MT 59936.

threat comes from a nonnative disease, white pine blister rust (*Cronartium ribicola*), which cannot be eradicated or controlled. Whitebark pine mortality exceeds 90 percent in much of the northwestern portion of its range (Kendall and Arno 1990). Mortality rates are lower in the drier climates to the south but may increase in the future. Although blister rust infected most five-needled pine populations by the 1930's, mortality has not stabilized. Blister rust is, in part, responsible for a rapid decline of whitebark pine in the Bob Marshall Wilderness Complex, MT, in the last 20 years (Keane and Morgan, these proceedings). Blister rust has been epidemic in sugar pine (*P. lambertiana*) in the southern Sierra Nevada Mountains, CA, since the 1970's where it had caused at least 25 percent mortality by 1985 (Kinloch and Dulitz 1990). Although the progress of the white pine blister rust epidemic is not fully understood, whitebark pine infection and mortality rates may increase if weather patterns change or if blister rust mutates to forms better able to survive dry climates.

The alarming loss of whitebark pine trees has broad repercussions for community and landscape processes. As whitebark pine declines, not only is mast for wildlife diminished (Kendall and Arno 1990) but vegetative patterns change. In areas of high whitebark pine mortality, lack of shelter was, in part, responsible for declines in associated subalpine fir in some areas (Keane 1992). Predicted changes in former whitebark pine communities include the absence of reforestation after disturbance in high-elevation, rocky, and windblown sites and lowered

tree-line elevations. Finally, the hydrology of large areas will be altered as snow accumulation changes with vegetation.

Natural resistance of the original whitebark pine population to blister rust is extremely low. While there are no direct data on the resistance of whitebark pine, only one western white pine (*P. monticola*) tree in 10,000 is rust resistant (Bingham 1983; Hoff and others, these proceedings). Since whitebark pine is more susceptible to blister rust than western white pine, the number of resistant whitebark pine trees is likewise less than 0.0001 percent. While blister rust is not expected to extirpate whitebark pine rangewide or even at most high-hazard sites because of the presence of resistance (Hoff and others 1980), isolated populations may become extinct where mountain pine beetle (*Dendroctonus ponderosae*) kill the remaining resistant whitebark pine. Using techniques developed in the successful program to breed rust-resistant western white pine, the USDA Forest Service is investigating the feasibility of developing rust-resistant whitebark pine. Based on their experience with western white pine, a program to develop resistant whitebark pine is expected to be successful (Hoff 1991).

Because whitebark pine is fire dependent in many areas, fire suppression poses another threat. Prior to human intervention, the average natural fire intervals in whitebark pine stands were 50 to 350 years (Arno and Weaver 1990). Despite natural fire policies, a seral whitebark pine stand would now burn once every 3,000 years (Arno 1986). In mixed-species stands where it is most

Table 1—Distribution and status of whitebark pine (PIAL¹) in North American National Park areas

Park area	Vegetation map?	Area with PIAL	Blister Rust? Absent/Present/Unknown	PIAL status
United States				
Big Hole NB	N	PIAL rare	A ²	unknown
Crater Lake NP	Y	unknown	P	>45% mortality ³
Glacier NP	Y	unknown	P	>90% mortality ⁴
Grand Teton NP	Y	unknown	U PIAL, PIFL	low mortality
Lassen Volcanic NP	Y	unknown	P PILA, PIMO; U PIAL	low mortality
Mount Rainier NP	Y	unknown	P PIMO, PIAL	Blister rust/mature PIAL: 92% infection; 43% dead ⁵
North Cascades NP	Y	3,922 ha ⁶	U	unknown
Olympic NP	N	unknown	P PIMO; U PIAL	poor reproduction
Sequoia-Kings Canyon NP	Y	unknown	P PIBA, PILA, PIMO	healthy
Yellowstone NP	Y	88,500 ha ⁷	U PIAL, PIFL	low mortality PIAL
Yosemite NP	Y	12,727 ha ⁸	P PILA; A ² PIAL, PIMO	healthy
Canada				
Banff NP	Y	300 ha	U	unknown
Jasper NP	Y	57,730 ha	U	no apparent threats
Kootenay NP	Y	unknown	U	unknown
Waterton Lakes NP	Y	3,990 ha	P PIAL, PIFL	serious mortality; extent unknown

¹PIAL = *Pinus albicaulis*; PIBA = *P. balfouriana*; PIFL = *P. flexilis*; PILA = *P. lambertiana*; PIMO = *P. monticola*.

²Absence assumed but no surveys conducted.

³From Jackson and Faller (1973).

⁴From Kendall and Arno (1990).

⁵Figures from survey of Sunrise Ridge Trail on August 10, 1992 (Hoff 1992).

⁶From Agee and others (1985).

⁷From Renkin and Despain (1992).

⁸From Jan Van Wagtenonk (1992).

valuable to bears and red squirrels (*Tamiasciurus hudsonicus*), whitebark pine is being replaced by shade-tolerant conifers in the absence of fire. Lack of fire has also increased whitebark pine mortality from mountain pine beetle and dwarf mistletoe (*Arceuthobium* spp.) (Kendall and Arno 1990). Fire suppression creates even-aged lodgepole pine (*P. contorta*) stands, which can support massive buildups of pine beetles that spill over into adjacent whitebark pine forests. Fire is a primary regulator of the frequency and intensity of dwarf mistletoe infection. Efforts to enhance the resistance of whitebark pine to blister rust should go hand-in-hand with ensuring conditions that maintain whitebark pine on the landscape. Thus far, despite widespread natural fire policies, the political constraints on prescribed fire mean most are controlled.

Park Service ability to deal with these threats is limited by how little we know of whitebark pine communities. Of 15 parks with whitebark pine, most had basic vegetation maps but only half knew the amount of area covered by whitebark pine (table 1). Where available, the whitebark pine coverage figures are not necessarily comparable. Some estimates only included areas where whitebark pine was dominant or codominant, while others included the area of all communities with whitebark pine present.

Because none of the parks had actually surveyed whitebark pine, its status in most areas was based on casual, at times out-dated, observation or was unknown. For example, the whitebark pine mortality estimate for Glacier National Park (>90 percent; table 1) was based on observations made in the early 1970's during a search for blister rust-resistant trees. Rocky Mountain National Park, CO, lists whitebark pine as present, but it is unlikely to occur so far south of its range and was probably confused with limber pine (*P. flexilis*). Although blister rust was verified as present in eight parks, because most park staffs were unfamiliar with blister rust, its presence was unknown or assumed absent in seven parks. Few parks had information on the effects of fire suppression in their whitebark pine communities.

Whitebark pine forests in National Parks have received little research attention. Canadian Parks Service reported no ongoing research in whitebark pine communities. In the United States, only Yellowstone National Park is currently conducting whitebark pine research. Some studies on postfire succession and fire effects on soil seed banks in Yellowstone National Park include whitebark pine stands. Yellowstone National Park personnel have monitored cone production in whitebark pine stands since 1981 and will survey those trees for blister rust this year. No other parks are conducting or sponsoring research or monitoring of whitebark pine.

RESTORATION POLICY

The vast losses of whitebark pine and the possibility that selectively bred whitebark pine will be available in the future raise some interesting questions for park managers. One challenge will be to determine what action is appropriate under these circumstances. Canadian Parks Service policy prescribes active intervention when "...natural processes have been altered by man and

manipulation is required to restore the natural balance" (Parks Canada 1979). NPS policy (National Park Service 1988) explicitly provides for active management to reverse the loss of whitebark pine. Policy states that the Service "...will strive to protect the full range of genetic types (genotypes) native to plant and animal populations in the parks by perpetuating natural evolutionary processes and minimizing human interference with evolving genetic diversity." The National Park Service will strive to restore native plants if "the species was substantially diminished as a result...of human-induced change...."

Park use of planting stock with enhanced resistance to rust is also clearly appropriate. Policy specifies "where a natural area has become so degraded that restoration with native species has proven unsuccessful, improved varieties or similar native species may be used" (National Park Service 1988). For park restoration projects, resistant stock development should be sensitive to maintaining pristine gene pools. "Whenever possible, revegetation efforts in natural zones will use seeds, cuttings, or transplants representing species and gene pools native to the ecological portion of the park in which the restoration project is occurring" (National Park Service 1988). General guidelines to prevent genetic contamination during vegetation restoration projects are beginning to emerge, but more specific guidelines await species-specific genetic research (Potter and Kurth 1992).

In other North American natural areas, introduced disease pests have devastated native forest trees such as American chestnut (*Castanea dentata*), flowering dogwood (*Cornus florida*), and butternut (*Juglans cinerea*). The exotic fungus, Chinese chestnut blight (*Endothia parasitica*), has killed all mature American chestnut trees (present on approximately 9 million acres) in North America since its introduction around 1900 (Langdon and Johnson 1992). Early attempts to control the disease and develop a resistant hybrid of Oriental and American chestnuts were not successful. Current efforts are backcrossing hybrids to yield stock with few "Oriental" traits, but it remains to be seen if the stock is resistant. Dogwood anthracnose (*Discula destructiva*), first found in North America in the 1970's, can kill all flowering dogwood (*Cornus florida*) at sites favorable to this introduced fungus. Another exotic fungus, butternut canker (*Seriococcus clavigeneti-juglandacearum*), caused 80 percent declines in butternut in North and South Carolina since the early 1970's (Anderson 1990) and suppressed nut crops in Great Smoky Mountains National Park (Langdon and Johnson 1992). Apparently resistant flowering dogwood from Catoctin Mountain Park and putatively resistant butternut from throughout its range are currently undergoing screening to verify resistance. Resistant stock would be used for introduction to natural populations and for further breeding work (Langdon and Johnson 1992).

National Park Service policy guiding genetic conservation is rapidly evolving. Langdon and Johnson (1992) felt that the appropriateness of using hybrids (such as those being developed for the American chestnut) for restoration of natural zones had not been established. However, a report clarifying Park Service policy (Keystone Center 1991) stated, "Restoration of native species is encouraged where...the restored species most nearly approximates

the extirpated species, and the species disappeared because of human-induced impacts to the population or ecosystem. Exotic species may not be introduced into natural zones of parks except where they are the nearest living relatives of extirpated native species...."

Use of rust-resistant whitebark pine stock for restoration in natural park zones is more straightforward. The efforts to develop resistant whitebark pine focus on speeding natural selection processes and do not involve hybridization or genetic engineering. In the face of the devastating loss of whitebark pine in many areas, use of these materials clearly would be in line with National Park Service policy. Moreover, to ensure that park genotypes are preserved in the breeding program it would be in the Park Service's best interests to be actively involved with the rust-resistance program.

However, because natural selection will no doubt differ from our best attempts to mimic it (in the breeding program), I believe there is also value in having areas where whitebark pine communities are left undisturbed to respond to the changes wrought by humans. Practically speaking, this will be easy to achieve since it will be logistically impossible to intervene in much of whitebark pine's range.

MANAGEMENT OPTIONS

Long-lived and slow-growing, whitebark pine trees are 50 to 100 years old before they begin to produce significant cone crops. Thus, whitebark pine stands are especially slow to recover from damage and slow to respond to management measures (Kendall and Arno 1990). Until fire is allowed to play its historical role in whitebark pine habitats and a high level of resistance to blister rust is achieved, whitebark pine will continue to decline or persist in many areas at very low levels.

We can expect to lose (or may have already lost) some small, isolated populations. In areas of high mortality, surviving trees represent only a subset of the original genetic pool. Park Service action strategy must recognize whitebark pine's special attributes and should be based on evaluation of the trade-offs of various management alternatives. A viable program should contain a combination of the following options and recommendations.

Restoration and Revegetation

Management options for general restoration of whitebark pine are:

1. Where fire suppression has caused the decline of whitebark pine, assess historical and present whitebark pine forest composition. Prepare sites for regeneration with management-initiated burns or manual removal of competing species. In natural fire zones, ease prescriptions so that natural fires will be allowed to occur in whitebark pine communities.

2. Rely on natural regeneration. Regeneration may fail to occur or may be very slow if seed sources are beyond the range of Clark's nutcrackers (*Nucifraga columbiana*) or are rare and scant.

3. Replant seed or seedlings of wild or resistant stock.

The factors affecting whitebark pine establishment are only beginning to be studied (McCaughy 1990). If successful, planting will speed reestablishment of whitebark pine. Planting resistant varieties on highly productive sites will accelerate growth and presumably result in early cone production.

Rust Resistance

Management options for dealing with rust-resistance issues are (Hoff 1991; Hoff and others, these proceedings):

1. No intervention. Allow natural processes to develop rust-resistant whitebark pine and restore whitebark pine communities. This may be a better selector of the various resistance mechanisms, but will require a great amount of time given whitebark pine's slow growth and maturation. Vegetation and animal communities will be dramatically altered for an extremely long time. This option may retain more genetic diversity than would a breeding program; however, genetic variation will decline if some small populations are lost or are greatly diminished.

2. Propagate and plant stock from surviving trees found in areas of high blister rust mortality. These materials are available now and any resistance present is a result of natural selection. This would mesh well with a seed bank program.

3. Manage natural-selection stands. In high blister rust hazard areas with high whitebark pine seedling density, allow natural selection to act on naturally regenerating stock. Shorten generation times by removing competing species. The advantages and disadvantages discussed for the no-intervention option hold true here. Another beneficial aspect is that the stock or seed for outplanting will be adapted to local conditions. It is debatable whether clearing competing species is appropriate in National Parks. However, if parks do not implement this option, park genetic stock will not be part of this important component of any plan developed for whitebark pine conservation.

4. Breeding program. One option is to collect wind-pollinated seed or cross pollinate trees in situ that exhibit some resistance to blister rust, germinate resultant seed, and infect seedlings with rust to select resistant types. The surviving seedlings would be outplanted, but some would be used to establish seed orchards. Repeat for several generations for resistant seed stock. Another option is to collect scion wood from resistant trees, graft to nursery root stock, test for resistance and induce flowering, and cross with other resistant types. Although these programs may be less successful in selecting for resistance than nature would be, they will generally reduce the time required to develop a high degree of rust resistance (65-100 years vs. hundreds of years). A breeding program could be designed to preserve genotypes from any targeted area and thus preserve representatives from populations at risk of being lost.

RECOMMENDATIONS

A number of recommendations for the management of whitebark pine on National Park Service lands can be made at this time.

1. Inventories and monitoring are recognized needs not yet fully realized by National Parks. Most National Parks with whitebark pine have not surveyed the extent and status of whitebark communities (table 1). We need to learn how much whitebark pine now exists and how much has been lost to various causes. Resistant trees should be located and marked.

2. Research genetic and adaptive variation. Because whitebark pine is wind-pollinated and seed is cached by Clark's nutcrackers up to 23 km from the seed source (Vander Wall and Balda 1977), total genetic variation in whitebark pine populations may be relatively high and, because of this constant genetic mixing, patterns of adaptive genetic variation may be relatively broad. That notwithstanding, genetic variation should be established to provide guidance for park restoration programs.

3. In areas where it is unknown, determine the fire history of whitebark pine stands. Study how to reintroduce fire to whitebark pine habitats or how to mimic its effects in the variety of habitats where whitebark pine occurs. Apply results to an experimental management program.

4. Support research on white pine blister rust damage and mortality rate equilibrium points for whitebark pine populations throughout its range.

5. Establish managed natural-selection stands for all whitebark pine populations at risk.

6. Support and collaborate with on-going efforts to develop rust-resistant stock. Develop guidelines for selecting genetic stock for inclusion in a breeding program that will meet Park Service mandates.

7. Seed banks. Collect and store seed to represent the breadth of genotypic, phenotypic, and geographic variation. Collection from small, isolated populations should be a priority. Seed stored under optimum conditions can remain viable for 30 to 100 years or more and represent insurance against catastrophic loss in natural settings.

8. Develop a comprehensive strategy for the conservation of whitebark pine in cooperation with other land management agencies and conservation organizations. One component should include the end of practices that remove whitebark regeneration in clearcuts and burns. The reverse, eliminating whitebark pine's competitors, should be adopted.

CONCLUSIONS

While whitebark pine is not alone in its need of attention in our quest to preserve biodiversity, it is under siege and we know little about it. High-mountain ecosystems are particularly vulnerable to disturbance. Thus, whitebark pine will be more susceptible than most species to the effects of global climate change, acid precipitation, and other forms of air pollution and should serve as a sensitive monitor of subtle environmental disturbance. Whitebark pine research and conservation will require coordinated action between various agencies and members of the conservation community. I urge agencies to conduct basic inventories of our subalpine environments and create a comprehensive conservation strategy for whitebark pine before more genetic material is lost. Because of their preservation missions, National Parks must be key players in conserving this as well as other species at risk.

ACKNOWLEDGMENTS

I am indebted to R. Hoff for extensive, invaluable discussions on whitebark pine genetics and management options for the development of rust resistance. Thank you to S. Woodley for information on the status of whitebark pine in Canadian National Parks. R. Keane, L. Kurth, W. McCaughey, and W. Schmidt provided valuable comments on an earlier draft.

REFERENCES

- Agee, J. K.; Pickford, S. G.; Kertis, J.; Finney, M.; de Gouvenain, R.; Quinsey, S.; Nyquist, M.; Root, R.; Stitt, S.; Waggoner, G.; Titlow, B. 1985. Vegetation and fuel mapping of North Cascades National Park Service complex. Seattle, WA: National Park Service Cooperative Park Studies Unit, College of Forest Resources, University of Washington: 17,59.
- Arno, Stephen F. 1986. Whitebark pine cone crops; a diminishing source of wildlife food? *Western Journal of Applied Forestry*. 1(3): 92-94.
- Arno, Stephen A.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.
- Arno, Stephen A.; Weaver, Tad. 1990. Whitebark pine community types and their patterns on the landscape. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 997-105.
- Bingham, R. T. 1983. Blister rust resistant western white pine for the Inland Empire: the story of the first 25 years of the research and development program. Gen. Tech. Rep. INT-146. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 45 p.
- Habeck, James R. 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier Park, Montana. *Northwest Science*. 43(2): 65-73.
- Hoff, R. J.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. *European Journal of Forest Pathology*. 10: 307-316.
- Hoff, Ray. 1991. [Personal communication]. October 10. Moscow, ID: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Hoff, Ray. 1992. [Personal communication]. August 17. Moscow, ID: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Hutchins, H. E.; Lanner, R. M. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Jackson, M. T.; Faller, A. 1973. Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. *Ecological Monographs*. 43: 441-461.
- Keane, R. T. 1992. [Personal communication]. December 8. Data on file at U.S. Department of Agriculture, Forest

- Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory, Missoula, MT.
- Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. In: International Conference on Bear Research and Management: Proceedings. Madison, WI: International Bear Association. 5: 166-173.
- Kendall, K. C.; Arno, S. F. 1990. Whitebark pine—an important but endangered wildlife resource. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-30; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 264-274.
- Keystone Center. 1991. Final consensus report of the Keystone policy dialogue on biological diversity on Federal lands. Keystone, CO: The Keystone Center. 96 p.
- Kinloch, B. B.; Dulitz, D. 1990. White pine blister rust at Mountain Home Demonstration State Forest: a case study of the epidemic and prospects for genetic control. Res. Pap. PSW-204. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 7 p.
- Langdon, K. R.; Johnson, K. D. 1992. Alien forest insects and diseases in eastern USNPS units: impacts and interventions. George Wright Forum. 9: 2-14.
- McCaughy, Ward W. 1990. Biotic and microsite factors affecting *Pinus albicaulis* establishment and survival. Bozeman, MT: Montana State University. 78 p. Dissertation.
- National Park Service. 1988. Management policies. Washington, DC: U.S. Department of the Interior, National Park Service: 4:1-11.
- Ogilvie, R. T. 1990. Distribution and ecology of whitebark pine in western Canada. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 54-60.
- Parks Canada. 1979. Parks Canada policy. Ottawa, ON: Parks Canada, Department of Indian and Northern Affairs. 68 p.
- Potter, R.; Kurth, L. 1992. Interim genetic guidelines for restoration projects, Glacier National Park. Glacier National Park Report. West Glacier, MT: U.S. Department of the Interior, National Park Service. 6 p.
- Renkin, R. A.; Despain, D. G. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. Canadian Journal of Forest Research. 22(1): 37-45.
- Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16(1977): 123-160.
- Van Wagtendonk, Jan. 1992. [Personal communication]. July 20. Yosemite National Park, CA: U.S. Department of the Interior, National Park Service.
- Vander Wall, S. B.; Balda, R. P. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecological Monographs. 47: 89-111.

Research Needs



International Workshop
St. Moritz 1992

RESEARCH NEEDS IN WHITEBARK PINE ECOSYSTEMS

Wyman C. Schmidt

Abstract—Whitebark pine (*Pinus albicaulis*) ecosystems occupy high elevations over a large geographic area in mountains of the Western United States and Canada. Interest in these ecosystems has increased dramatically, partly because whitebark pine forests are very important for survival of endangered grizzly bears (*Ursus arctos horribilis*). Research has been sporadic. The advent of Ecosystem Management is creating new demands for information concerning ecological processes and the need to manage on a landscape scale. This paper outlines obvious gaps in knowledge of this important species and ecosystem as expressed by researchers and land managers at a recent whitebark pine symposium and workshop.

Research in whitebark pine (*Pinus albicaulis*) ecosystems is relatively new in North America. Whitebark pine forests were largely ignored by managers and researchers in the United States, and even more so in Canada. Most of this research has been done in the last 10 to 15 years, primarily in the Greater Yellowstone Ecosystem in Idaho, Wyoming, and Montana (McCaughey and Weaver 1990).

Important research has been under way in other areas within the range of whitebark pine, but the overwhelming importance of this species in the Yellowstone Ecosystem prompted the acceleration of research in that area. These forests harbor grizzly bear, mountain sheep, elk, and a host of other wildlife species; provide late-season water for valleys below; provide expansive views and solitude for the high-mountain visitor; and, to a lesser extent, provide some of the wood products for North America.

Research in whitebark pine forests has largely been done as a labor of love by individual scientists from a broad spectrum of disciplines, not as a centralized, fully coordinated research program. Researchers—from various universities, the U.S. Department of Agriculture, Forest Service, U.S. Department of the Interior, National Park Service, and other public and private individuals—have a professional scientific bond but few administrative ties. For most researchers, whitebark pine studies were a small segment of their total research effort.

During most of the 20th century there has been a gradual transition from custodial to more proactive management of National Forests. For most of the first half of this

century, efforts were concentrated on fire, insect, and disease protection. Fire protection was especially effective, at least in the short term. Custodial management was gradually converted to proactive management with greater emphases on production and regulation of timber, range, wildlife, and water, because timber and range management practices emphasized those tangible commodities. Most proactive management was in the lower to mid-elevation areas; high-elevation site management remained largely custodial.

In the 1950's there was a gradual transition toward management that emphasized more balanced resource management goals. Recreation became a significant consideration. This drive for balance in forest uses culminated in the Congressionally mandated Multiple-Use Act of 1964 for national forests. This law continues to be in effect. Many other public and private land managers have also adopted the multiple-use concept.

In the late 1980's and early 1990's, the Forest Service added ecological criteria for managing national forests. These practices, now termed Ecosystem Management, include increased emphases on sustaining long-term productivity, retaining biological diversity, sustaining ecological functions and integrity, including social and economic values in planning, and incorporating landscape-scale considerations into management practices. A particularly important goal is the continual acquisition and use of the best scientific facts and concepts dealing with the various biological, social, and economic functions of the ecosystem. Thus, very strong partnerships between management, research, education, and the public must be formed and are key to effective implementation of Ecosystem Management.

The initiation of Ecosystem Management led to realization that the scientific base needed for managing our various North American ecosystems is often fragmented, incomplete, difficult to locate, not integrated, and inadequately interpreted. This was particularly apparent in high-elevation forests where whitebark pine is a major constituent.

In response to the accelerating demand for scientific information about whitebark pine forests, we sponsored a major symposium (Schmidt and McDonald 1990) and several workshops were held to examine in depth these high-mountain areas. Our objective was to assemble scientists, educators, managers, and the public interested in this subject. In the process we attempted to ferret out and present the best available information.

The 1989 symposium on whitebark pine (Schmidt and McDonald 1990) closed with a chapter asking "Where Do We Go From Here?" A portion of that chapter, as well as many of the individual papers in the proceedings, discussed knowledge gaps and research needs in whitebark

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Wyman C. Schmidt is Project Leader of the Subalpine Forest Ecology and Silviculture Research Unit, Intermountain Research Station, Forestry Sciences Laboratory, Forest Service, U.S. Department of Agriculture, Montana State University, Bozeman, MT 59717-0278.

pine ecosystems. From these sources, I extracted the research needs pointed out by the authors—mostly researchers but also some managers. Because research needs varied widely in scale, I stratified them into different levels from micro to macro (gene to global).

There were over 160 research needs suggested, but many were essentially duplicates. I categorized the suggested research needs into nine different levels: Gene, Tree, Stand, Forest, Ecosystem, Landscape, Regional, Continental, and Global. The level assigned the various suggestions was a subjective assignment by this author, but most were fairly definitive and easily categorized. Under each of the different levels I paraphrased the various research needs, some of which were mentioned by one or several authors. The following section lists those needs.

RESEARCH NEEDS

Each heading is the level to which research needs were assigned. The statements below it are expressions of what we need to know to fill gaps in existing knowledge of whitebark pine ecosystems.

Gene

- Genotypic and adaptive variation of whitebark pine.
- Genetic resistance to blister rust of whitebark pine.
- Monoterpene differences between geographic areas.
- Effects on the genetic base by blister rust and fire suppression.

Tree

- How tree growth dynamics relate to soil chemical and physical properties and geomorphology.
- Site, stand, and area relationships to mountain pine beetle, secondary bark beetles, and cone and seed insects.
- Regeneration mechanisms and requirements of whitebark pine.
- Techniques for propagating whitebark pine for a variety of site conditions.
- How to better identify and predict cone crop periodicity.
- Physiological tolerances and ecological characteristics, including water and nutrient relationships, of species adapted to major disturbances, such as mining.
- Characteristics of mycorrhizal and nitrogen-fixing symbionts of associated subalpine species.

Stand

- Rehabilitation methods for dealing with disturbances due to mining, fire, grazing, and high-use recreation.
- Physiological and morphological response information in relation to competing tree species.
- Interrelationships of various resources, such as water, forage, cover, and cone production.
- Successional relationships at treeline and downward into mixed species stands.
- How to explain the diversity of growth forms.

- Role of domestic animals, such as cattle, sheep, and horses in the introduction of undesirable plants or other organisms.

- Combinations of tree species and silvicultural prescriptions needed to maintain viable squirrel populations.
- Squirrel population relationships to cone crops of whitebark pine.

- Harvesting, thinning, and burning practices needed to favor whitebark pine establishment and growth.

- In grizzly bear areas where cone production is critical, what ecological habitats should be featured in research and management.

- Stand structure, or species composition, critical to squirrel behavior and population.

- Amount of whitebark pine needed to attract nutcrackers; level of cache recovery by nutcrackers or other predators.

- Relationship of stand conditions, such as those created by thinning for increasing cone production, to snow redistribution.

- Management strategies needed (and to be avoided) to protect and enhance fisheries in high-altitude lakes and streams.

- How we can use this information in reclamation projects.

Forest

- Better methods for protecting forests from insect, disease, and fire problems.
- Ecological effects of fire suppression and how to reintroduce fire.
- How to develop strategies for protecting rare and endangered species.
- How fragile or elastic these forests are in the long term.
- What conflicts there are between domestic stock and wildlife, such as grizzly bear and elk.
- Specific squirrel/bear/whitebark pine relationships in different ecological habitats.
- How whitebark pine fits in the hydrologic cycle.
- How to set management objectives.

Ecosystem

- How to develop monitoring techniques that capitalize on sensitive environmental indicators in zones where whitebark pine is a component.
- More quantifiable parameters and equations for building simulation models for all projected resource use.
- More about habitat requirements in these forests for large mammals such as bighorn sheep, goats, and moose.
- How to devise monitoring and long-term permanent plots to use this ecosystem to detect climate change.
- How to increase communication between managers and researchers.

Landscape

- Stand structure relationships at different altitudes, latitudes, geographic areas, and ecotypes.

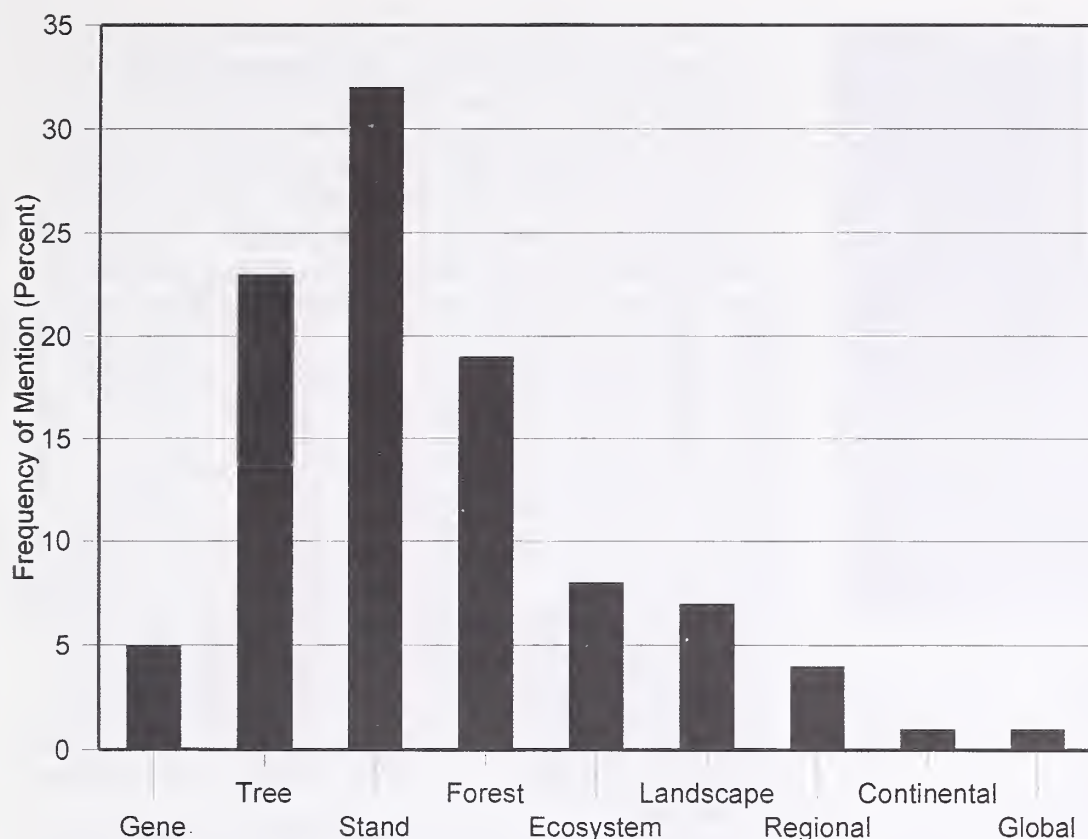


Figure 1—Whitebark pine research needs from micro to macro levels (gene to global), based on frequency of mention by all authors at the whitebark pine symposium.

- How to effectively utilize artificial intelligence (AI), geographic information systems (GIS), and various models for evaluating landscape-scale activities, including micro-to-macro extrapolation methods.

- How to relate natural mosaics to human activity mosaics.

- How to better manage information to more effectively expedite transfer from research to managers.

Regional

- Information from a survey of whitebark pine conditions throughout its range, including insect and disease conditions.

- How to develop more replicable information throughout the whitebark pine range.

- The history of whitebark pine throughout its range.

- Fire history throughout the whitebark pine range.

Continental

- How to better distribute research throughout the geographic range of whitebark pine.

Global

- Better methods of detecting potential climate change effects on whitebark pine survival.

DISCUSSION

Authors at the 1989 whitebark pine symposium described research needs most often at the stand level, but needs at the tree and forest level were a close second and

third (fig. 1). These are based on the frequency of mention at the various levels. Each mention reflects an individual author's intimate knowledge of a particular level and recognition of research needs at that level. A bias may exist because tree, stand, and forest are the levels at which most forestry research has traditionally been conducted (figs. 2, 3, 4). But, in spite of emphases at the stand and tree levels, there was a wide distribution of research needs suggested across the spectrum from gene to global levels (fig. 1).



Figure 2—Individual tree growth is relatively slow on high-elevation sites where whitebark pine grows. How are tree growth dynamics related to soil, site, and insect and disease conditions?



Figure 3—Whitebark pine stands, composed of mature trees such as these in the Absarokee Mountains of Montana, produce the seeds so important to the survival of the grizzly bear, squirrel, and nutcracker. What stand conditions optimize conditions for these wildlife species?

A subsequent workshop (McCaughey and McDonald 1993) that updated some of the information presented at the whitebark pine symposium of 1989 also included a query of research needs. The scale of needs from gene to global level was essentially the same as that found at the 1989 symposium. Research needs expressed at the 1993 workshop reflected particular concern with the threat of significant blister rust invasion and mortality in the Greater Yellowstone Ecosystem.

Some of the authors at the 1989 symposium were from the management community, and they addressed the knowledge gaps they are facing when they have to make difficult forest management decisions. Most managers felt that researchers should increase the scope of their research. Although they saw many of the same needs expressed by the researchers, managers tended to express more concerns about needs at the ecosystem and landscape levels (fig. 5). This is not surprising, given the recent emphases on Ecosystem Management that are being adopted by most of the major public land management agencies in the United States. This holistic approach to management presents a significant new challenge to the research, education, and management communities.

It is obvious that there are enough research needs in whitebark pine ecosystems to charter a major ecological research program. Fortunately, the evolution of electronic methods for handling large amounts of data, and developing conceptual, mathematical, and visual models, may help speed solutions to ecological problems. Although the challenge is great, the mood and tools for tackling Ecosystem Management are being developed. The whitebark pine ecosystem is a good candidate for testing these methods.

It should be emphasized that the research needs described in this paper help set the direction and priority of research, but other factors come into play. For example, just because a research need is mentioned most frequently does not necessarily mean that need has the highest priority. An example is the severe mortality problems associated with blister rust. If we cannot solve the blister rust mortality problem, some of the other whitebark pine research becomes almost academic. Ideally, everyone working with whitebark pine would like to see a comprehensive and integrated research program throughout the range of whitebark pine in North America.



Figure 4—Whitebark pine forests occupy scenic high-elevation areas. Disturbances, such as this windthrow, create small openings where nutcrackers cache whitebark pine seeds, resulting in subsequent regeneration. What are the regeneration mechanisms and requirements for whitebark pine?

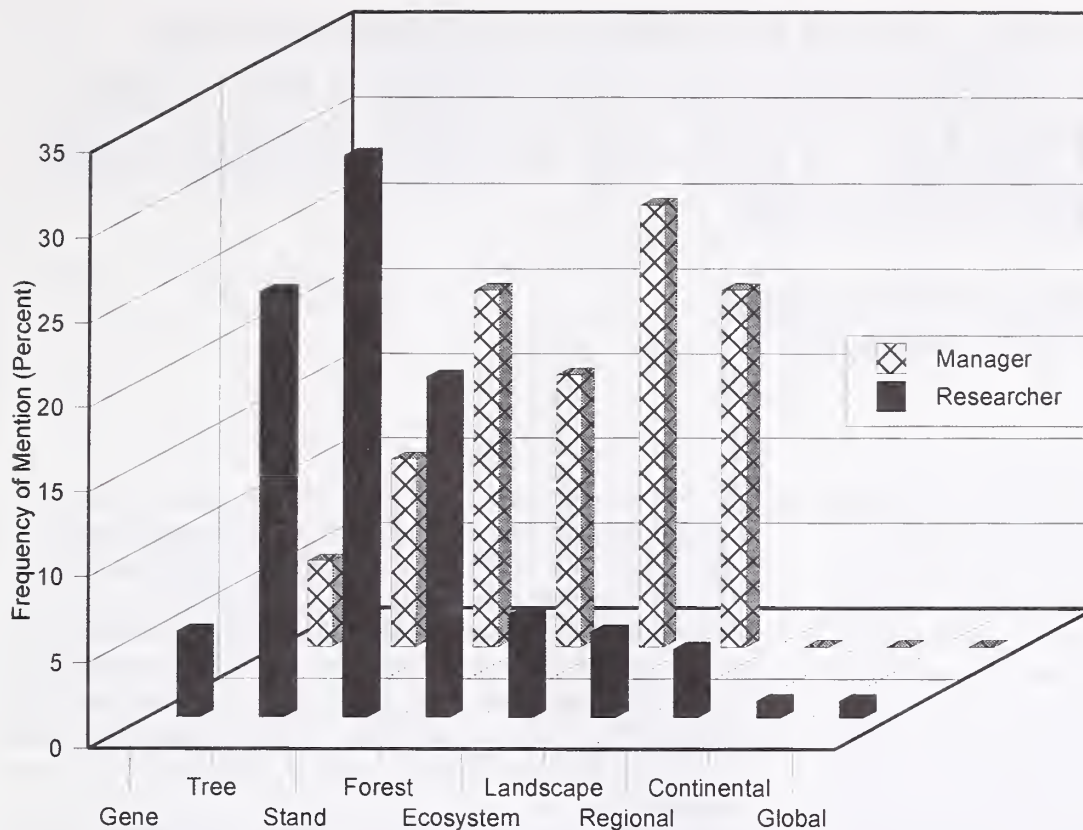


Figure 5—Whitebark pine research needs from micro to macro levels (gene to global), based on frequency of mention by authors from the research and management communities at the whitebark pine symposium.

Realistically, we know that will not happen. As Lanner (1993) stated in his editorial concerning the threat to the survival of whitebark pine: "Each organization has a very few dedicated researchers putting mere fractions of their time into relevant whitebark pine research, but the need greatly outstrips their ability to fill it." Lanner recommended that the Forest Service and Park Service assemble an "interagency commission to come to grips with the impending disaster now facing whitebark pine, and to give high priority to that research and program implementation deemed most promising." We have a national and international responsibility to meet these challenges.

REFERENCES

- Lanner, Ronald M. 1993. Is it doomsday for whitebark pine? *Western Journal of Applied Forestry*. 8(2): 47-48.
- McCaughey, Ward W.; McDonald, Kathy J. 1993. Management of whitebark pine ecosystems—an international and regional perspective: workshop proceedings; 1993 April 23; Bozeman, MT. Bozeman, MT: Intermountain Research Station, Forestry Sciences Laboratory, Montana State University. 56 p.
- McCaughey, Ward W.; Weaver, T. 1990. Reference guide to whitebark pine. In: Schmidt, Wyman C.; McDonald, Kathy J., comps. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 376-386.
- Schmidt, Wyman C.; McDonald, Kathy J., comps. 1990. Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 386 p.

PROBLEMS OF COMPREHENSIVE INVESTIGATION, UTILIZATION, AND REPRODUCTION OF RUSSIAN CEDAR PINE FORESTS

Vladislav N. Vorobjev
Nina A. Vorobjeva

Abstract—Cedar pine forests occupy vast areas in Russia and are composed of three types of pines: the Siberian stone (or cedar) pine (*Pinus sibirica* Du Tour), Korean pine (*Pinus koraiensis* Sieb. et Zucc.), and mountain pine (*Pinus pumila* [Pall.] Regel). All of these are stone pines and are pioneer tree species. Most of the paper discusses Siberian stone pine, the main stone pine species in Russia. These forests not only provide valuable raw materials, but other ecological values are increasingly being recognized. This paper describes cone and seed development and production, artificial reproduction, site and stand characteristics, seed morphology and chemistry, climatology, tree growth, and other characteristics of these stone pine trees and forests. Management implications are also discussed.

Cedar pine is the commonly used term for stone pine forests found in Russia. These forests are composed of three types of cedar pines: Siberian stone (or cedar) pine (*Pinus sibirica* Du Tour), Korean pine (*Pinus koraiensis* Sieb. et Zucc.), and mountain pine (*Pinus pumila* [Pall.] Regel). All these occupy about 40 million ha, with Siberian stone pine accounting for 90 percent of the total.

Cedar pine forests are of paramount importance for Russia. Cedars not only provide valuable raw materials, but they also play an ever-increasing role in ecology. Their stands are critical for conservation of water resources (on mountains and near sources of great Siberian rivers the Ob, the Irtysh, the Yenisei, and also around Baikal Lake) and they also serve to stabilize swamping processes (in the West Siberian Plain). Cedar pines are pioneer tree species known for their soil-cover protection function, especially for the subalpine zone.

ECOLOGICAL FORMS

Ecological conditions for Siberian stone pine growth vary by latitude and altitude. The trees of typical form grow at the altitude of the subalpine zone in North Altai where the elevation is 1,500-1,600 m. Other ecological forms include

the most important one, a mountain form (f. *coronans*). It is unlike trees of typical form and is comprised of second-value trees with dense crowns, especially in the zone of the male cone growth. Branches of this type of crown usually begin at ground level. The female zone of the crowns comprises less than 30 percent of total crown length. Development of generative and vegetative organs of this mountain form of Siberian stone pine begins a month later than those trees in the low part of the mountains. Cone crops are rare and small.

The mean length of f. *coronans* cones is 62-64 mm in years with good crops and 43-45 mm in years with bad crops. In bad crop years the cones are small and ball-like with a mean width of 38-40 mm and usually 20-30 large seeds (the weight of 1,000 seeds is 260-280 g). The cones have scales with a red hue. Most of the scales (40 percent) have a flat apophysis. The weight of 1,000 seeds is 170 ± 30 g in f. *coronans* and 240 ± 70 g in typical form trees in years with good crops. Seeding quality of f. *coronans* seeds is low, seed germinating capacity is less than 30-40 percent, and one-third of the seeds have no embryo.

F. *coronans* reproduction very seldom results from its own seeds. Instead, nutcrackers (*Nucifraga caryocatactes macrorhynchos* Brehm) carry seeds from lower elevation stands of the typical form of Siberian stone pine to the upper part of the mountains. The nutcracker seed distribution plays a significant role in the preservation of f. *coronans* areas. Correlation of this way of reproduction and growth of f. *coronans* with other subalpine forms has not been exactly determined. This problem is especially important for investigating ecology of growth and generative development of Siberian stone pine in the different altitude zones.

Another ecological form of Siberian stone pine is f. *nana* (elevation is 1,900-2,000 m). Trees here grow to about 10 m height, disperse as single trees or clumps, and do not form stands. The boundary of tree life form and the generative boundary of the species is here. Trees here bear few Siberian stone pine cones and have only about 15-20 female shoots in the crown. Oval cones are about 50 mm in length, have no more than 20-30 seeds, and they mature only rarely.

The upper end of the ecological row is f. *humistrata* (other name is f. *depressa*). It is sterile. This form is a small tree or shrub 2-3 m in height. F. *humistrata* forms the upper forest boundary (elevation is 2,000-2,400 m).

Mean height of trees of these four ecological forms of Siberian stone pine decreases with increasing elevation: 35, 17, 10, and 2 m. Characteristics of the typical form and f. *coronans* stands at different elevations are shown in table 1.

Paper presented at the International Workshop on Subalpine Stone Pines and Their Environment: The Status of Our Knowledge, St. Moritz, Switzerland, September 5-11, 1992.

Vladislav N. Vorobjev is Head and Nina A. Vorobjeva is a Researcher of the Institute for Ecology of Natural Complexes, The Academy of Sciences, Siberian Division, Akademicheskoy pr. 2, Akademgorodok, Tomsk, 634055, Russia.

Table 1—Characteristics of stands of the Kiga ecological line

Number of sample plot	Site index, forest type	Elevation	Tree story	Content ¹	Stand density	Stand age	Mean height	Mean diameter	Growing stock
		m				Year	m	cm	m ³ /ha
2a	I, large-grassy	450	1	3PS(I)	0.15	300	35	80	90
				7PS(II)	.44	210	32	58	296
			2	9AS	.36	130	17	25	90
				1Bs	.03	90	20	39	10
				Unit PS	—	90	12	10	2
8a	II, green-mossy fern	1,250	1	10PS	.76	270	29	67	470
			2	10AS	.35	130	19	21	103
				Unit PS	—	130	13	13	4
13	V, large-grassy with <i>Leuzea carthamoides</i>	1,800	1	10PS	1.15	210	17	37	340

¹Abbreviations: PS—*Pinus sibirica* Du Tour; AS—*Abies sibirica* Ldb.; Bs—*Betula* sp.

The change of stand characteristics and the formation of Siberian stone pine ecological forms follows climatic indexes. Yearly air temperature changes from +1.4 °C to −2.8 °C, the sum of temperatures above 10 °C decreases from 1,400 °C to 630 °C, and the sum of precipitation increases from 450 to 980 mm with elevation increases from 450 to 2,000 m.

The isolation of Siberian stone pine ecological form is confirmed by hemotaxonomy data (Vorobjev and others 1971). The investigation of monoterpene contents in oleoresin shows differences of quantity between the typical form and the *f. nana* trees as well as in the different altitude zones (table 2).

α -pinene and β -pinene are decreased and the quantity of Δ^3 -karene and β -phellandrene is increased in the typical form of Siberian stone pine with increasing elevation in the mountains. We observed the analogical change of monoterpene content of Siberian stone pine trees in connection with resin-tapping done for the purpose of obtaining resin substances for different industrial tasks. This is related usually to increasing tree stability due to influence of different factors, including the enhancing of oleoresin-forming activity.

It is believed that distinguishing monoterpene content in *f. nana* trees, unlike typical tree form, will be analogical. That is, the quantity of α -pinene and β -pinene will be less and Δ^3 -karene will be more. It appears that the monoterpene content in the oleoresin changes in the other direction.

In *f. nana* the contents of α -pinene, and β -pinene especially, are more and Δ^3 -karene and β -phellandrene are less when compared with data for the typical form (elevation is 1,250 m).

These changes have formed the simplified monoterpene content in *f. nana* oleoresin. Three basic hydrocarbons (α -pinene, β -pinene, and Δ^3 -karene) are contained in *f. nana*. The total sum is 97 percent in *f. nana* and 88.6 percent in the typical form of Siberian stone pine. The other direction of synthesis of monoterpene and its simplified content in *f. nana* is possibly related to the change for the worse of ecological condition.

Our study provides perspective in this direction. Other studies are needed to develop this perspective in different regions and in different species of cedar pines. These types of investigations are appropriate, especially in mountains where ecological forms can be distinguished very easily.

ECOLOGICAL FACTOR INFLUENCE

The influence of ecological factors on development of Siberian stone pine trees and their physiological processes is illustrated by a good visible example of lipid accumulation in seeds. Table 3 shows accumulative dynamics in seeds for trees of typical form, *f. coronans*, and *f. nana* (elevations are 450, 1,650, and 1,850 m, respectively).

It is obvious that lipid accumulation is significantly late in the subalpine form. The seeds have standard lipid content (60 percent) at the end of July (7/29) in the typical form of Siberian stone pine, in the third week of September (9/22) in *f. coronans*, and at the beginning of October (10/2) in *f. nana*. The lipid content of the subalpine ecological form reaches the optimal value in crop years. It confirms the physiological capacity of its seed for reproduction.

Table 2—Monoterpene content in oleoresin of *Pinus sibirica* Du Tour Typical Form (T) and *Pinus sibirica* Du Tour *f. nana* Beissn. (N) (percent)

Monoterpene	T		N
	450 m elevation	1,250 m elevation	(1,900 m elevation)
α -pinene	50.5 \pm 1.5	39.1 \pm 1.2	47.9 \pm 1.5
Kamphene	.8 \pm .2	1.2 \pm .2	.7 \pm .2
β -pinene	11.0 \pm .4	9.6 \pm .4	120.3 \pm .6
Δ^3 -karene	27.6 \pm .8	39.5 \pm 1.2	128.8 \pm .8
Mirtsen	1.5 \pm .2	1.4 \pm .2	1.6 \pm .2
Limonene	2.0 \pm .2	.6 \pm .2	1.5 \pm .2
β -phellandrene	6.4 \pm .3	8.4 \pm .4	1.2 \pm .1

¹Values are very different from mean in typical form.

Table 3—Dynamics of lipid content in Siberian stone pine seeds in mature process (percent of absolute dry substance)

Elevation	20.6	26.6	2.7	9.7	22.7	29.7	6.8	13.8	13.9	22.9	27.9	2.10	10.1
<i>m</i>													
450	8.1	21.6	29.2	47.6	51.2	61.6	62.2	62.5	64.2	63.5	64.1	—	—
1,650	—	3.0	4.9	7.6	17.4	29.6	43.3	57.0	60.3	61.0	61.6	64.6	62.5
1,850	—	2.5	4.9	6.9	17.4	27.0	42.4	52.2	53.2	56.4	58.4	61.1	57.5

On the whole, the dynamics of the maturing of Siberian stone pine seeds are characterized by slow lipid accumulation, then the intensification of this process in July, and some decreasing of total lipid content after the determination of optimal correlation of fatty acids. This phenomenon, known as "over-ripening," is characteristic of Siberian stone pine as well as many oily plants.

The Siberian stone pine and other cedar pine seeds have great value as food in Russia. General physical and chemical characteristics of Siberian stone pine seed have been published in a collective monography (Vorobjev and others 1979) and also in some papers (Rush 1974; Rush and Lizunova 1969). This is shown in table 4.

Together with the high lipid content the seeds have many amino acids, including irreplaceable acids as well as many macro- and micronutrient elements, and especially valuable vitamins B₁, E, and F. The Siberian stone pine seeds for B-vitamin activity are more preferable than the other cedar pines and the oily plants (table 5). Also, Siberian stone pine seeds are valuable for macro- and micronutrient elements (table 6).

The quantitative contents of known elements of Siberian stone pine seeds are similar to mountain pine seeds, and they have more phosphorus, iodine, and cobalt than Korean pine seeds. The significant quantity of potassium, sodium, copper, and zinc in the Siberian stone pine seeds determines its high quality.

The high content of iodine in Siberian stone pine and mountain pine seeds has special importance for those regions where trees have endemic goiter.

A comparison of the seed content from the plain and mountain Siberian stone pine forests shows an increased content of manganese, silicon, boron, nickel, and phosphorus, as well as iron in the middle part of the mountains. The seeds from different plant regions can be distinguished by increased content of potassium, zinc, molybdenum, aluminium, and iodine. In the upper part of the mountains the content of phosphorus, copper, zinc, and boron, the most important elements determining viability of seeds, is decreased. The content of magnesium, iron, and silicon also is less diminished high in the mountains.

On the whole, the changes of mineral content of seeds are related to their physiological and biochemical maturation, ecological conditions of tree growth, and geochemical indexes of cedar pine in the widespread regions.

CONE AND SEED CROPS

The investigations of cone and seed crop dynamics have a special meaning for study of growth and generative development of Siberian stone pine trees. The method of retrospective calculation of crops for the last 100 years or more

Table 4—Characteristics of Siberian stone pine seed

Characteristic	Mean	Range
Physical indexes		
Length (mm)	10.4000	8.9000 - 11.9000
Width (mm)	7.7000	6.0000 - 8.7000
Seed weight (mg)	200.0000	153.0000 - 317.0000
Nucleus weight (mg)	96.0000	78.0000 - 125.0000
Shell (percent of weight)	51.6000	51.5000 - 58.9000
Nucleus (percent of weight)	46.6000	41.0000 - 48.6000
Seed coat (percent of weight)	1.8000	1.5000 - 2.4000
Density (g/cm ³)	.8700	.8500 - .8800
Specific volume (g/cm ³)	1.1500	1.1400 - 1.2000
Chemical indexes		
Nitrogen-bearing substance (percent of absolute dry substance):		
total nitrogen	2.9000	2.0800 - 3.2700
protein nitrogen	2.6100	1.9300 - 3.0100
nonprotein nitrogen	.2900	.1500 - .3800
Total nitrogen of unlipid remainder (percent of absolute dry substance)		
protein nitrogen	4.8300	4.6000 - 5.1500
nonprotein nitrogen	.7000	.6000 - .8300
nitrogen of dense remainder	2.1700	1.8800 - 2.3800
Free amino acids (mg percent of absolute dry substances)		
Cytine	10.5000	Traces - 19.5000
Lisine	15.3000	2.2000 - 35.7000
Histidine	17.1000	13.0000 - 25.7000
Arginine	15.5000	12.0000 - 26.2000
Aspartic acid	23.3000	15.5000 - 30.2000
Serine	9.8000	3.5000 - 14.3000
Glycine	4.5000	Traces - 11.2000
Glutamic acid	50.3000	46.4000 - 87.9000
Threonine	16.7000	10.9000 - 18.7000
Alanine	30.7000	28.7000 - 44.4000
Proline	24.1000	17.9000 - 35.7000
Tyrosine	17.3000	14.5000 - 32.1000
Methionine	13.4000	Traces - 42.9000
Valine	8.4000	5.8000 - 13.0000
Tryptophan	Traces	Traces - Traces
Phenylalanine	13.5000	Traces - 34.0000
Leucine-isoleucine	14.2000	8.6000 - 25.6000
Protein acids		
Lisine	1.2000	0.6000 - 1.4000
Histidine	.9000	.6000 - 1.4000
Arginine	5.9000	3.1000 - 7.5000
Aspartic acid	4.9000	1.8000 - 5.9000
Threonine	1.0000	.8000 - 1.5000
Serine	2.1000	1.6000 - 2.1000
Glutamic acid	4.6000	2.9000 - 7.3000
Proline	1.6000	.7000 - 2.2000
Glycine	1.7000	.7000 - 1.7000
Alanine	1.9000	.7000 - 2.1000
Valine	1.1000	.9000 - 2.2000
Methionine	.6000	.2000 - .8000
Isoleucine	1.6000	.8000 - 2.0000
Leucine	2.0000	1.3000 - 3.1000
Tyrosine	1.5000	.8000 - 1.7000
Phenylalanine	1.4000	.8000 - 1.6000
Tryptophan	.6000	0.6000

(con.)

Table 4 (Con.)

Characteristic	Mean	Range
Contents of carbohydrate nature (percent of absolute dry substance)		
Glucans:		
cellular tissue	2.2000	1.9000 - 2.4000
starch	4.5000	1.9000 - 8.2000
dextrine	2.3000	2.1000 - 2.5000
pentosanes	1.8000	1.6000 - 2.2000
Sum of easily soluted carbohydrates:	6.2000	3.3000 - 14.3000
sucrose	5.1000	2.1000 - 12.4000
raffinose	3.4000	.3000 - 4.7000
glucose	.1000	.1000 - .3000
fructose	.2000	.1000 - .8000
Lipids		
Lipid content (percent of absolute dry substance)	64.0000	50.0000 - 76.0000
Acid content in oil (percent)		
nonsaponificated substances	1.1200	.7800 - 1.3500
saturated acids	5.7600	5.1300 - 6.4200
unsaturated acids:		
oleic acid	15.7600	11.3300 - 22.2200
linoleic acid	57.2400	53.1400 - 59.1100
linolenic acid	21.2200	16.5800 - 24.6400
Mineral substances (P-Fe in mg percent, Mn- in mg/kg)		
P	481.8000	428.4000 - 716.1000
Mg	529.4000	258.9000 - 559.8000
K	489.3000	350.9000 - 503.3000
Na	107.1000	83.9000 - 114.3000
Ca	48.4000	35.1000 - 49.6000
Fe	2.3000	2.0000 - 4.9000
Mn	5.4000	5.2000 - 11.3000
Cu	1.5000	1.3000 - 3.9000
Zn	12.1000	7.1000 - 15.1000
Mo	.2000	.1000 - .3000
Si	2.3000	2.0000 - 3.7000
Al	5.3000	3.0000 - 6.4000
I	.5000	.3000 - .9000
B	.0002	.0001 - .0017
Ni	.0300	.0090 - .0470
Co	.0500	.0390 - .0980
Pb	.0300	.0270 - .0640
Sr	.0004	.0001 - .0029
Ag	.0300	.0190 - .0910
Aches content (percent)	2.5000	2.4000 - 2.7000
Chemical indexes of oil		
Acid number (mg KOH)	1.4100	1.1800 - 1.7100
Saponification value (mg KOH)	196.9000	189.7000 - 201.3000
Reihert-Meissl's number	1.3300	1.1100 - 1.5400
Polanske's number	.4100	.2900 - .5900
Gube's iodine number	166.6000	158.2000 - 177.2000
Rhodanic number	97.1000	94.2000 - 100.3000
Phosphatide content (percent)	1.3400	1.0000 - 1.6500
Vitamins (mg percent):		
A (carotene)	Traces	Traces
B ₁ (thiamine)	.6500	.5500 - .6900
B ₂ (riboflavin)	.9300	.8400 - 1.2100
C (ascorbic acid)	Traces	Traces
E (tocopherols):		
in seeds	10.1000	9.2000 - 32.8000
in oil	54.8000	50.1000 - 65.0000
F (unsaturated fatty acid) (percent)	94.3000	93.6000 - 94.9000

Table 5—Vitamin content in seeds (mg percent of absolute dry substance)

Plant species	Thiamine	Riboflavin	Total
<i>Pinus sibirica</i> Du Tour	0.242	0.933	1.175
<i>Amygdalus nana</i> L.	.111	.730	.841
<i>Pistacia vera</i> L.	.149	.639	.788
<i>Pinus koraiensis</i> Sieb. et Zuss.	.236	.210	.446
<i>Pinus pumila</i> (Pall.) Regel	.049	.263	.312
<i>Juglans regia</i> L.	.096	.186	.282

or 33 years, and longer. Relationship of the cycles is very complicated in different latitudes and within each latitude. Examples of likeness and unlikeness of longer cycles are available. The differences are observed especially in shorter cycles. Except for the direct effect of weather condition on the development of generative organs, solar activity influences crop dynamics. This problem is studied widely in dendrochronology. Studies of the effect of solar activity on seed-bearing of forest trees, including Siberian stone pine, is at the initial stage.

Study of the crop dynamics is planned for long-range predictions. You can see in figure 2 that solar activity has a direct and positive influence on shoot growth. After its active increment the cycle of good crops of Siberian stone pine begins.

MORPHOPHYSIOLOGY

Knowledge of the morphophysiological state of separate tissues and organs during the processes of morphogenesis is one of the basic conditions needed to determine the role of growth in the cone-bearing and regulation of periodicity of Siberian stone pine crops. It is necessary to study the morphological and physiological regularities of growth and

Table 6—Content of macronutrient and micronutrient elements in cedar pines (Russ 1974)

Element ¹	<i>Pinus sibirica</i>	<i>Pinus pumila</i>	<i>Pinus koraiensis</i>
P	481.8000	586.2000	341.9000
Mg	529.7000	317.4000	682.4000
K	489.3000	452.8000	549.6000
Na	107.1000	113.8000	278.4000
Ca	48.4000	49.6000	82.4000
Fe	2.3000	4.1000	11.3000
Mn	5.4260	8.3120	9.0110
Cu	1.4790	1.8150	14.2130
Zn	12.1320	8.6520	11.7160
Mo	.1730	.0930	—
Si	2.3230	3.1440	8.6520
Al	5.2780	8.1560	9.9130
I	.4590	.6820	.0170
B	.0002	.0001	—
Ni	.0470	.0110	.1610
Co	.0470	.1430	.0380
Pb	.0290	.0031	—
Sr	.0004	.0080	.0001
Ag	.0290	.0210	—

¹P-Fe in mg percent, Mn-Ag in mg/kg.

was worked out in our institute for ecology of natural complexes in Tomsk (Vorobjev 1979). Data for Siberian stone pine crop dynamics for the latitudinal profile of the West Siberia area can be obtained by using this method (fig. 1).

It has been determined that the cone crop dynamics have cycles of different duration: for 3 years, 10 or 11 years, 28

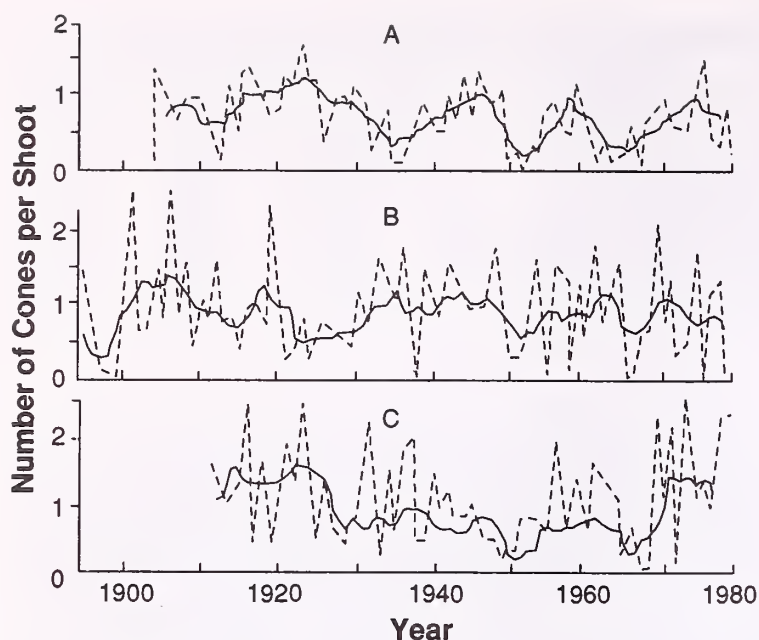


Figure 1—Cyclicity of Siberian stone pine crops for latitude lines of West Siberia: A—67°N, B—60°, C—56°N.

sexualization and their relationship as a condition that switches one development program to another. Modern views consider this switching the result of trophic, hormonal, and genetic interactions (Chaylakhyan 1984).

Participation of each of these factors in determining Siberian stone pine sexualization was recently proved by the peculiar physiological and biochemical characteristics of the different sex shoots. These data show that the peculiarities of generative shoots are a function of the differences between hormonal and trophic substances in total content, correlation between their separate form, composition of quality, and the seasonal dynamics rhythm.

The same changes are also found in cases of increasing or decreasing of sexual display in shoots or the total organism. For example, increasing female shoot reproduction in our study was correlated with decreases of oligosaccharides in the needles and increasing content in the shoot axis in

the period of vegetation end (Vorobjeva 1973). The degree of the sexual signs and, therefore, the cone-bearing state of Scotch pine, are correlated with dynamics, content, metabolism direction, and intensity of differences in needles, buds, and shoot axes. But these alterations are not clearly related to quantitative changes of physiological characteristics (Mosin and Savina 1985; Samsonova and Bolgova 1985).

This is all shown by small studies of the individual role of each substance and the order of their action in the processes of sexualization. There is a need to mark the absence of correlation between biochemical characteristics and the morphological state of the organs and organism. For example, the carbohydrate accumulation in buds for the initiation of generative primordia or in shoot axes in the finished growth period may be a result of change in the rate of the following stages of growth. Both of these processes are factors that lead to sexualization. But the association of changes in this factor with changes of the biochemical conditions do not give concrete results. Moreover, evaluation of changes of biochemical conditions as only one aspect of the metabolism prevents display of the processes leading directly to sexualization. This situation does not allow use of physiological characteristics as the mark. Therefore, it is necessary to intensify work in this direction to determine any connection with morphology.

Besides, the characteristics of generative shoots that we have today reflect the summary metabolism changes under influence of initiation of the floral stems, development of generative structure, and the generative load. This also does not permit display of the conditions of each stage of morphogenesis.

The carbohydrate metabolism and morphological stage of apical female shoots were studied in common. This showed that the nutrition of the 1- and 2-year cones change the content, the activity, and the turn of direction of the soluble carbohydrate reserve during the processes of growth or reservation. Such changes are different during the development of the reproductive structures and growth of shoots. These changes do not influence the direction of morphogenesis but make the stage of development longer. The meaning of this, however, is not clear because the boundary value of growth for the display of the sex is not known. This knowledge is needed for each form of trees and stage of ontogenesis. Knowledge of the ontogenesis behavior of each phenotype is necessary to objectively mark their productivity and posterity growth.

Knowledge about morphological changes of individual forms of trees is also limited. Analyses of the relationship of growth and sex of the shoot are confirmed by the correlation between sexualization with all values composing the growth, and the absence of direct dependence of the differences in the rate of variability on the stage as well as the critical value for change of stage (table 7). The role of each of the factors is inconsistent. Sex type of the tree has no direct correlation with the growth characteristics. But indirect correlation is the result of interaction of the growth with other organized factors (Fx).

From this point of view, the data analysis says much about metamere variability of vegetative development and shorter morphogenesis of female type trees. These trees also conserved a higher rate of evocation changes in the beginning of reproduction.

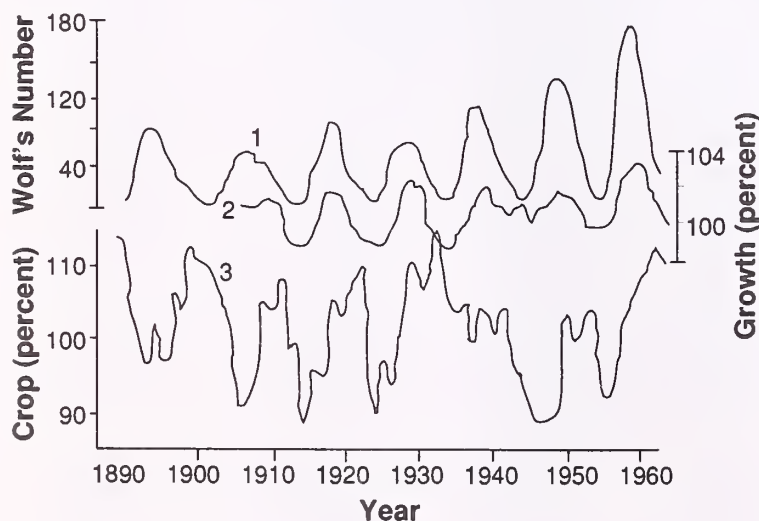


Figure 2—Solar activity (1), apical growth of female shoots (2), and crop value of Siberian stone pine (3) in the subalpine subzone in Gorny Altai.

Table 7—Growth of shoots on trees of different sexual types

Shoot Fb	Tree Fa			F fact
	Female	Male	Asexual	
Branch age (year)				
Vegetative	41.20	37.80	54.40	—
Vegetative	69.30	74.40	88.90	—
Female	80.80	86.10	100.60	—
Axis length (cm)				
Vegetative	3.19	2.53	3.14	Fa - 2.18
Vegetative	3.85	8.26	8.65	Fb -53.80
Female	11.16	13.54	14.94	Fx - 9.93
Axis diameter (cm)				
Vegetative	0.53	0.50	0.53	Fa - 0.47
Vegetative	.70	.79	.84	Fb -59.10
Female	1.41	1.46	1.27	Fx -13.20
Parenchyma of bark/medulla (B/M)				
Vegetative	5.50	6.50	7.10	—
Vegetative	4.10	3.80	3.80	—
Female	1.80	2.10	1.90	—
Brachyblasts on axis				
Vegetative	18.70	18.80	19.30	Fa - 2.04
Vegetative	21.00	37.80	45.90	Fb -27.50
Female	50.80	63.70	71.80	Fx - 6.25
Auxiblasts on axis of first bud				
Vegetative	0.50	0.80	0.56	Fa - 1.46
Vegetative	.75	2.10	1.80	Fb -27.50
Female	.80	1.90	1.40	Fx - 6.25
Auxiblaston on axis of second bud				
Female	2.40	2.60	2.50	Fa - 2.04
Generative germs on axis				
Female	2.70	2.10	2.00	—

Higher metamere variability correlates with increased frequency of double bud formation during the vegetation season in the period of virgin development. The biological regularities of the relationship of resin-forming, and generative and growth processes in Siberian stone pine are used as a theoretical principle for working out optimal combinations of elements for industrial complexes.

FOREST MANAGEMENT

The comprehensive investigation of Siberian stone pine forests of many regions of Siberia by its scientists, including the authors of this paper, for the last 30 years shows that management in these forests must be distinguished from management of other forests.

Traditional practices of forest management are planting, receiving, utilization, and reproduction of wood. Now added to these purposes are the observations of many ecological demands that do not change the classic scheme and techniques of forest management. Previously, the main aim of this forest management was wood production. Its basic elements were mainly technical exploitability ages and felling ages,

traditional cleaning cutting and major produce, clear cutting, and "continuous" artificial regeneration.

Mostly, these elements are unfit for Siberian stone pine forests. New theoretical principles and new practices of forest management are required.

First of all, the purpose of forest management in Siberian stone pine forests is not the wood only, but the comprehensive utilization of all forest resources including wood, nuts, oleoresin, berries, mushrooms, furs, game, and ecological and esthetic values. Technical exploitability ages, felling ages, and major produce should not be used as criteria for marking. Every tree, every stand must be comprehensively examined, but not only on the basis of wood growing stock. Trees must be felled in conformance with these value estimations. Thus, qualitative evaluations of every stand and every tree in Siberian stone pine forests must be made, but the middle-statistical method of forest felling on the basis of the correlation of age, growing-stock, and increment wood is not used.

The classic methods of forest management in Siberian stone pine forests are not acceptable because Siberian stone pine is not an ordinary tree. This tree has valuable nuts and many other specific properties. Based on felling ages of Siberian stone pine under previous management principles, this tree must be felled at 160 years old to obtain the best wood. But Siberian stone pine's most intensive cone-bearing occurs in trees about 160 years old. Because of this connection it is not possible to fell the Siberian stone pine at this age. Thus, felling schedules must be determined by the state of cone bearing and other comprehensive properties.

The new theoretical principles of forest management in Siberian stone pine forests have been developed by our Institute. They are published in some monographs (Isaev 1985; Vorobjev 1983) and as general instruction in "The Manual for Organization and Forest Management in Siberian Cedar Pine Stands" (Isaev 1990). Now, in Siberia great experimental works are being conducted on a comprehensive estimation of Siberian stone pine forests, on their selection and growth, and on the creation and control of new felling technology. The practical resolution of these problems will permit the rational use of the Siberian stone pine resources, the conservation of the better part of the Siberian stone pine forests for ecological purposes, the reproduction of valuable gene sources, and the enhancement of recreation uses.

Perhaps, many new theoretical principles of Siberian stone pine forest management may be of use with other cedar pines, other cedars, or other conifers. We confirmed the validity of many of our suppositions when we visited Korean pine forests of the Great Hingan in China.

The problem of reproducing Siberian stone pine forests was believed very difficult and insoluble for a long time. In the 1960's, problems with seed stratification were solved. At first results were not positive, but now the technology of seed stratification is worked out.

The problem of growing Siberian stone pine seedlings has also been solved, and there is a great reserve of planting material in nurseries. But this material is not sold because the politics of reproducing Siberian stone pine forests have changed during the last few years. At first the main method of reproducing Siberian stone pine forests, as well as other coniferous forests, was forest plantations. This method has

Table 8—Intrapopulation structure of crop capacity of stand (cones per tree)

Statistical index	Tree		Number of cones		Number of female shoots per tree	Cv of crop for 10 years	Number of trees		Number of cones	
	Diameter	Age	Per tree	Per shoot			Per ha	Percent	Per ha	Percent
	cm	Years								
Class I: 0 - 0.50										
\bar{x}	38.8	186.5	15.6	1.06	14.4	50.8	21	30	300	8
m	1.2	5.4	1.2	.04	1.0	1.8				
C_v	22.7	20.3	54.6	27.80	49.0	25.8				
Class II: 0.51 - 1.00										
\bar{x}	51.1	211.0	45.7	1.37	34.7	38.4	20	30	900	22
m	1.1	4.4	1.3	.05	1.4	1.5				
C_v	15.8	14.7	19.3	18.90	28.3	27.0				
Class III: 1.01 - 1.50										
\bar{x}	55.7	206.0	72.3	1.41	51.6	37.1	12	17	900	22
m	2.2	5.7	2.1	.04	1.6	1.5				
C_v	21.2	14.8	15.6	15.30	16.3	21.6				
Class IV: 1.51 - 2.00										
\bar{x}	69.9	223.7	99.2	1.36	74.4	38.6	9	13	900	22
m	3.9	7.0	1.8	.04	2.6	1.7				
C_v	27.5	14.3	8.4	15.10	15.8	20.0				
Class V: more 2.01										
\bar{x}	62.9	222.2	150.6	1.58	96.5	35.1	7	10	1,000	26
m	1.5	5.8	6.5	.05	5.2	2.9				
C_v	10.1	10.8	17.9	14.70	22.3	34.4				
Mean										
\bar{x}	51.2	205.5	58.7	1.31	42.8	41.6	69	100	4,000	100
m	1.1	5.8	3.4	.02	2.2	.9				
C_v	27.8	17.1	73.8	23.40	67.0	29.7				

proven unsuitable during 30 years. Forest plantations were created by planting small 2-year-old seedlings in harvested areas that had become overgrown with heavy grass cover and intensive growth of birch and aspen. Because the forest plantation was overgrown, it died. The necessary care of these plantations was absent.

Now, the main method for reproducing forests is by conserving understory trees in Siberian stone pine forests during cleaning operations. Particular hopes in Siberia and other regions of Russia rest on an initial thinning of Siberian stone pine undergrowth under cover of birch and other leaf-bearing trees. Siberian cedar pine normally reproduces naturally as a result of tree succession in grassy forest types. Our aim is to assist this process.

There are millions of hectares of natural generation of Siberian stone pine under birch and Scotch pine overstory. For the last century, at least in Siberia, the intensive macrocycle of Siberian stone pine generation has developed. It includes much movement of the Siberian stone pine boundary area in the north and in the mountains. Theoretical principles of optimal Siberian stone pine forest reproduction are the doctrine for reproduction and age dynamics that Russian scientists developed in the Ural (Kolesnikov and Smolonogov 1960; Smolonogov 1990).

Reproducing Siberian stone pine today in great volumes depends mainly on correct technology of felling in leaf-bearing forests. Now, our Institute has decided to accomplish the task using Finland logging machines.

Artificial reproduction of Siberian stone pine is restricted mainly to the establishment of the forest plantations for different purposes. The selection forest inventory, the selection choice of plus trees, and the control of posterity and reproduction are made for this. The selection is conducted for growth rate, resin productivity, and crop capacity.

SELECTING CROP FORMS

The choices for selecting crop forms from the population are great. For example, the data for intrapopulation structure of crop capacity (table 8) show that trees of V class were of specific interest. They exceed the crop capacity for the average tree in the stand by more than two times. These trees have high cone-bearing energy (number of cones per shoot) and well-developed female storey. They comprise one-fourth of the stand and 77 percent of the crop. This is more than four times the production of all low-crop trees. The better crop capacity trees have good growth indexes too—their diameters are more than the mean diameters of sample

Table 9—Characteristics of plus trees related to crop capacity

Number of trees	Tree		Number of cones			Number of cone-bearing shoots per tree	Cv of crop for 10 years	Selection rank
	Diameter	Age	per tree	per 1 cm of diameter	per shoot			
	cm	Years						
17	52	198	160	3.1	1.9	83	13.6	2.8
29	64	228	154	2.4	1.9	81	29.0	2.2
30	64	180	191	2.9	1.7	115	42.2	2.6
95	67	198	170	2.5	1.3	129	37.6	2.2
98	56	190	199	3.4	1.8	107	28.5	3.1
107	60	210	163	2.7	1.6	99	31.8	2.4
128	68	190	197	2.8	1.4	142	59.7	2.5
Mean for class	60	199	176	2.8	1.7	108	34.6	2.5
Mean for stand	51	205	58	1.1	1.3	43	41.6	1.0

trees by 20 percent. Examples of crop capacity plus trees and the individual variability of crop structure can be seen in table 9.

These trees are now reproduced in selection centers. The basic center is at our Institute near Tomsk. Valuable selection plantations are created by planting seedlings of 50 cm length with close root systems in brackets in our center. We are sure that this technology will result in good quality and conservation of Siberian stone pine forest plantations.

Solution of these problems is the main emphasis of work on artificial reproduction of Siberian stone pine in Siberia.

REFERENCES

- Chaylakhyan, M. Kh. 1984. Regulations of high plant flowering. In: Hormonal regulation of ontogenesis in plants. Nauka, Moscow: 9-27. [In Russian].
- Isaev, A. S., ed. 1990. The manual for organization and forest management in Siberian cedar pine stands. Moscow. 120 p. [In Russian].
- Isaev, A. S., ed. 1985. Siberian cedar pine forests of Siberia. Nauka, Novosibirsk. 256 p. [In Russian].
- Kolesnikov, B. P.; Smolonogov. 1960. Some principles of age and regeneration dynamics in Zaural'skoe Priob'e cedar pine forests. In: Problems of cedar. Novosibirsk: 21-33. [In Russian].
- Mosin, V. I.; Savina, L. G. 1985. Physiological and biochemical peculiarity of Scotch Pine for different sexual type. In: Sexual reproduction of conifers. Novosibirsk: 59-60. [In Russian].
- Rush, V. A. 1974. Biochemical characteristics of cedar pine seeds. In: Biology of seed reproduction of western Siberian conifers. Nauka, Novosibirsk: 180-184. [In Russian].
- Rush, V. A.; Lizunova, V. V. 1969. Some principles of chemical composition of Siberian cedar pine seeds. Vegetational Resources. 5(4): 519-525. [In Russian].
- Samsonova, A. E.; Bolgova, T. B. 1985. Biochemical aspects of sexualization of Scotch Pine in the central forest-steppe region. In: Sexual reproduction of conifers. Novosibirsk: 60-62. [In Russian].
- Smolonogov, E. P. 1990. Ecological and geographical differentiation and dynamics of Siberian cedar pine in Urals and West Siberian Plain. Ural Div. USSR Acad. Sci. Publ., Sverdlovsk. 286 p. [In Russian].
- Vorobjeva, N. A. 1973. Peculiarity of carbohydrate metabolism in Siberian cedar pine from activation of reproductive processes. In: Sexual reproduction of conifers. Nauka, Novosibirsk: 210-213. [In Russian].
- Vorobjev, V. N. 1979. A method of retrospective study of seminiference dynamics in *Pinus sibirica* Du Tour. Bot. Zhurn. 64(7): 971-974. [In Russian].
- Vorobjev, V. N. 1983. Biological principles of comprehensive utilization in Siberian cedar pine forests. Nauka, Novosibirsk. 256 p. [In Russian].
- Vorobjev, V. N.; Dubovenko, Zh. V.; Pentegova, V. A. 1971. On hemotaxonomic characteristics of *Pinus sibirica* Du Tour mountain forms. Vegetational Resources. 7(4): 564-567. [In Russian].
- Vorobjev, V. N.; Vorobjeva, N. A.; Sviridenko, E. I.; Kolesov, V. M. 1979. Siberian cedar pine seeds. Nauka, Novosibirsk. 129 p. [In Russian].



Schmidt, Wyman C.; Holtmeier, Friedrich-Karl, comps. 1994. Proceedings—international workshop on subalpine stone pines and their environment: the status of our knowledge; 1992 September 5-11; St. Moritz, Switzerland. Gen. Tech. Rep. INT-GTR-309. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 321 p.

This proceedings is the product of the first international workshop on the five subalpine stone pines of the world—*Pinus albicaulis*, *P. cembra*, *P. koraiensis*, *P. pumila*, and *P. sibirica*. It includes 48 papers on the evolution and taxonomy, ecology, regeneration, growth, environmental factors, wildlife, forest structure and dynamics, forest management, and research needs of the stone pines. All five stone pines—one in North America and the other four in Europe and Asia—share similar flora and fauna and behave in similar ecological patterns.

KEYWORDS: *Pinus albicaulis*, *P. cembra*, *P. koraiensis*, *P. pumila*, *P. sibirica*, wildlife, bears, squirrels, nutcracker birds, stone pine ecology, regeneration, seed dispersal, taxonomy, genetics, growth, research needs

Schmidt, Wyman C.; Holtmeier, Friedrich-Karl, comps. 1994. Proceedings—international workshop on subalpine stone pines and their environment: the status of our knowledge; 1992 September 5-11; St. Moritz, Switzerland. Gen. Tech. Rep. INT-GTR-309. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 321 p.

Dieser Bericht ist das Ergebnis des ersten Internationalen Workshops über die fünf subalpinen Steinkieferarten der Erde—*Pinus albicaulis*, *P. cembra*, *P. koraiensis*, *P. pumila* und *Pinus sibirica*. Er enthält 48 Vorträge über die Evolution und Taxonomy, die Ökologie, die Regeneration, das Wachstum, die Standortfaktoren, das Tierleben, die Waldstruktur und -dynamik, die Waldbewirtschaftung und -pflege sowie den Forschungsbedarf. Die fünf Steinkieferarten - eine in Nordamerika und vier in Eurasien beheimatet - weisen viele ökologische Gemeinsamkeiten auf.

STICHWORTE: *Pinus albicaulis*, *P. cembra*, *P. koraiensis*, *P. pumila*, *P. sibirica*, Tierleben, Bären, Eichhörnchen, Tannenhäher, Ökologie, Regeneration, Samenverbreitung, Taxonomy, Genetik, Wachstum, Forschungsbedarf





The Intermountain Research Station provides scientific knowledge and technology to improve management, protection, and use of the forests and rangelands of the Intermountain West. Research is designed to meet the needs of National Forest managers, Federal and State agencies, industry, academic institutions, public and private organizations, and individuals. Results of research are made available through publications, symposia, workshops, training sessions, and personal contacts.

The Intermountain Research Station territory includes Montana, Idaho, Utah, Nevada, and western Wyoming. Eighty-five percent of the lands in the Station area, about 231 million acres, are classified as forest or rangeland. They include grasslands, deserts, shrublands, alpine areas, and forests. They provide fiber for forest industries, minerals and fossil fuels for energy and industrial development, water for domestic and industrial consumption, forage for livestock and wildlife, and recreation opportunities for millions of visitors.

Several Station units conduct research in additional western States, or have missions that are national or international in scope.

Station laboratories are located in:

Boise, Idaho

Bozeman, Montana (in cooperation with Montana State University)

Logan, Utah (in cooperation with Utah State University)

Missoula, Montana (in cooperation with the University of Montana)

Moscow, Idaho (in cooperation with the University of Idaho)

Ogden, Utah

Provo, Utah (in cooperation with Brigham Young University)

Reno, Nevada (in cooperation with the University of Nevada)

The policy of the United States Department of Agriculture Forest Service prohibits discrimination on the basis of race, color, national origin, age, religion, sex, or disability, familial status, or political affiliation. Persons believing they have been discriminated against in any Forest Service related activity should write to: Chief, Forest Service, USDA, P.O. Box 96090, Washington, DC 20090-6090.